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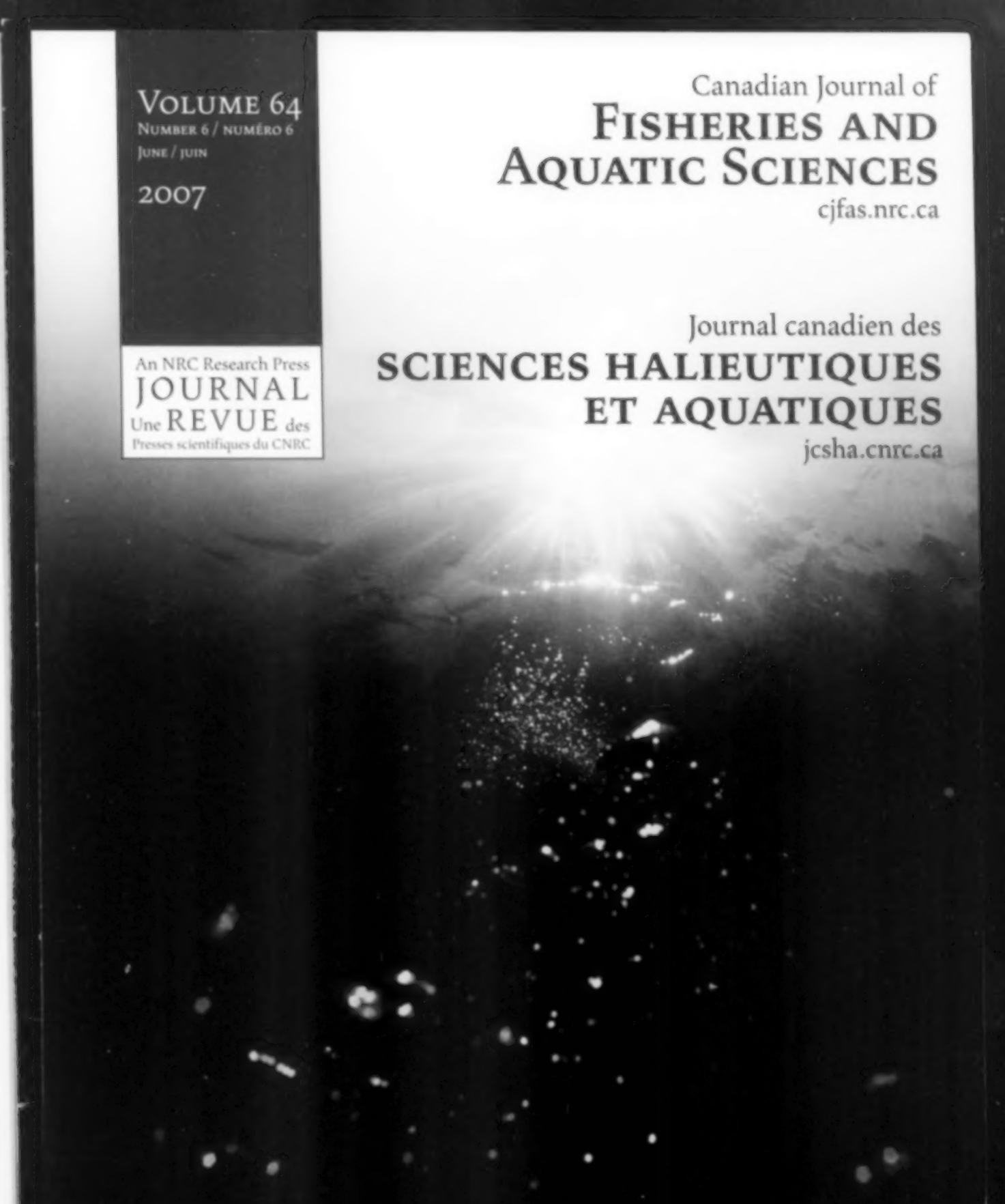

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The digestive and metabolic enzyme activity profiles of a nonmetamorphic marine fish species: effects of feed type and feeding level

Simon Gaston Lamarre, Nathalie Rose Le François, Hélène Lemieux, Inger-Britt Falk-Petersen, and Pierre Ulrich Blier

Abstract: We investigated activity levels of metabolic and digestive enzymes in Atlantic wolffish (*Anarhichas lupus*) and their relationships with growth, ration level, and type of food during the first 50 days after hatch. Newly hatched wolffish were divided among three experimental groups differing in feed and ration (formulated feed in excess (FF), a maintenance ration of *Artemia* (LA), and *Artemia* in excess (EA)) that generated different growth rates. A principal component analysis revealed that activities of the glycolytic enzymes lactate dehydrogenase (LDH) and pyruvate kinase (PK) were associated with mass gain, while those of the aerobic enzymes citrate synthase and aspartate aminotransferase (AAT), and digestive enzymes (lipase and trypsin) were related to time (days) after hatch. Food restriction or food type allowed the observation of a direct relationship between the activities of trypsin and those of associated metabolic enzymes AAT and glutamate dehydrogenase in the LA group (Pearson's R of 0.71 and 0.59, respectively), as well as between the activities of amylase and those of LDH and PK (Pearson's R of 0.62 and 0.48, respectively) in the FF group. The adaptative importance of these patterns during early development of wolffish and their relationship to feeding conditions are examined.

Résumé : Les effets de la croissance, du stade de développement, du type d'aliment et de la restriction alimentaire sur le niveau d'activité de certaines enzymes métaboliques et digestives ont été évalués chez le loup Atlantique (*Anarhichas lupus*) durant les 50 jours post-éclosion. Des taux de croissance différents ont été atteints avec succès chez des loups nouvellement éclos en utilisant une combinaison de différents types d'aliments et de taux d'alimentation: moulée commerciale en excès (FF), *Artemia* faible ration (LA) et *Artemia* en excès (EA). Une analyse en composantes principales a révélé que l'expression des enzymes glycolytiques (lactate déshydrogénase (LDH) et pyruvate kinase (PK)) est associée au gain en masse, alors que le développement des enzymes du métabolisme aérobie (citrate synthase et aspartate aminotransférase (AAT)) et des enzymes digestives (lipase et trypsine) est plus corrélé au temps depuis l'éclosion (exprimé en jours post-éclosion). La restriction alimentaire et le type d'aliment ont permis l'observation d'un lien direct entre l'activité de la trypsine et les deux enzymes associées, AAT et glutamate déshydrogénase (Pearson's R de 0,71 et 0,59, respectivement chez le groupe LA) et entre l'amylase, la LDH et la PK (Pearson's R de 0,62 et 0,48, respectivement). Les patrons de développement des enzymes en fonction des conditions nutritionnelles sont examinés en fonction de la stratégie adaptative.

Introduction

Extremely dynamic and complex processes of organ differentiation, morphogenesis, and growth take place as newly hatched fish gradually develop to become juveniles (Gisbert et al. 2002; Sala et al. 2005). Concurrently, during this period, fish will grow at a speed that they will never again accomplish during their life span (Power and Walsh 1992). Much research on this critical life stage for fish gravitates around the notion that mortality is very high,

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size-dependent, and, consequently, tightly coupled with growth and the availability of food resources (Sanderson and Kupferberg 1999). Newly hatched fish must rapidly acquire adequate feeding and swimming behaviours (i.e., efficient prey detection, capture, digestion, assimilation, and predator avoidance) to survive and thrive (Jobling 1995; Gawlicka et al. 2000). The interaction between metabolic activity and digestion is particularly crucial, since both components greatly influence growth rate (Blaikie and Kerr 1996; Karjalainen et al. 2003).

Catabolism of food is organized to efficiently harness the chemical energy of substrates for use in anabolic and other life-sustaining processes. During early life, the failure to meet nutritional needs because of inefficient or poorly developed ingestion, digestion, or assimilation processes will result in impaired growth, starvation, reduced viability, and ultimately death (Blier et al. 1997; Bureau et al. 2002). Thus, it has been suggested that complete functionality of the digestive organs (i.e., the availability of digestive enzymes and of key metabolic enzymes) could set substantial physiological limitations on the growth and (or) survival of juveniles (Blier et al. 1997; Lemieux et al. 1999; Lamarre et al. 2004). Accordingly, fast relative growth of the digestive organs was observed during early life in *Dentex dentex*, indicating the priority of the development of these organs for growth and survival (Santamaria et al. 2004; Sala et al. 2005).

Wolffishes (*Anarhichas lupus* and *Anarhichas minor*) have recently been identified as threatened species in Canada (Committee on the Status of Endangered Wildlife in Canada, www.cosewic.gc.ca), and both species are the focus of aquaculture research and development efforts in the northern hemisphere (Le François et al. 2002; Foss et al. 2004). Early life stages of wolffishes show strong similarities with those of salmonids, including large egg diameters (4–5 mm), large and apparently robust larvae (a size at hatch of 20–23 mm), precocious ontogeny, and active phototactic swimming behaviour (Pavlov and Moksness 1994). However, commercial and experimental wolffish juvenile production regularly presents high mortality during first-feeding operations (variable proportion of hatched larvae from particular families will never start feeding and die of starvation) (Falk-Petersen and Hansen 2003; Lamarre et al. 2004). For research purposes, newly hatched fish are usually presented with *Artemia* nauplii for 1–3 weeks and then weaned to dry feed granules (300–500 µm initially, then 500–800 µm) (Falk-Petersen et al. 1999). Commercial operations omit the live organism phase, and first-feeding larvae are offered a commercial feed composition (60% protein and 16%–18% lipid) immediately after hatch. Wolffish mortality is very low after the weaning period (3–4 weeks after hatch; Hansen and Falk-Petersen 2002).

The present study examined the development of digestive capacity and key energetic metabolic pathways in newly hatched Atlantic wolffish (*Anarhichas lupus*) given two types of food at different rations. We investigated the relationship of activities of selected enzymes to growth, developmental stage, and feeding regime. Monitoring the metabolic and digestive enzyme responses of fish to different rations and types of food will contribute to understanding the physiological impacts of restricted access to food, as well as the mechanisms used to cope with the pressures of variable food supply imposed by the environment (Collins and Anderson 1997; Lemieux et al. 2004; Weber and Bosworth 2005). This may also reveal valuable information on the nutritional needs of a given species (Gawlicka et al. 2000; Kolkovski 2001; Furne et al. 2005). To our knowledge, our study is one of the few, in addition to Lemieux et al. (2003), Segner et al. (1994), and Segner and Rösch (1998), to focus on the relationship between digestive capacity and the key enzymes of the related metabolic pathways in fish on restricted rations.

Materials and methods

Fish

Wild-fertilized Atlantic wolffish egg masses were collected in November 1998 from Conception Bay, Newfoundland and Labrador, Canada, by a team of professional divers and transferred to the Centre Aquacole Marin (Grande-Rivière, Québec, Canada). The egg masses were incubated in modified Heath tray incubators continuously supplied with seawater (average salinity and temperature 28 $g \cdot L^{-1}$ and 5 °C, respectively), and the eggs were regularly disinfected according to established protocols (Hansen and Falk-Petersen 2002). To obtain simultaneous hatching, gentle pressure on the egg mass was applied when a peak of hatching was observed (at around 980 degree-days). Previously hatched fish were excluded from this study. The fish were randomly distributed into three groups (two replicates per group), for a total of six groups of 150 fish each, placed into low-level raceways supplied with running, filtered seawater (growing surface of 30 cm^2 at 4–5 cm water depth). To avoid thermal stress at transfer, the temperature was gradually increased from 6 to 9–10 °C (1 $°C \cdot day^{-1}$) and maintained at that temperature for the duration of the experiment. All groups were fed enriched *Artemia* nauplii ($100 \cdot L^{-1}$) for the first 2 days to stimulate feeding behaviour. From day 4 through day 50, group LA (low ration *Artemia* concentration) and EA (excess *Artemia* concentration) received 50 $Artemia \cdot L^{-1}$ and 500 $Artemia \cdot L^{-1}$, respectively. The third group (FF) was fed formulated feed for marine fish (Nutramarine, Skretting) to excess. Care of the fish followed guidelines of the Canadian Council on Animal Care (www.ccac.ca).

Sampling and growth monitoring

A number of fish were sampled at hatch and at 1, 5, 10, 20, 40, and 50 days after hatch (DPH) during the experiment. Three fish from each tank were measured (total length, TL), weighed, and frozen at –80 °C until further analysis (a total $n = 126$ fish for enzyme analysis). A previous study had determined that the intestinal transit time of Atlantic wolffish kept at full salinity is approximately 12 h (Le François et al. 2004). Accordingly, fish were not fed for 12 h before sampling.

The specific growth rate (SGR) was calculated as

$$SGR(\% \cdot day^{-1}) = 100(\ln W_{t_2} - \ln \bar{X}_{W_{t_1}})(t_2 - t_1)$$

where W_{t_2} is wet weight at t_2, $\bar{X}_{W_{t_1}}$ is average weight of the replicate at t_1, t_1 is the time at the beginning of an interval, and t_2 is time at the end.

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The absolute and relative volumes of the digestive tract are indicators of the capacity of ingestion and digestion (Lilja 1997). The allometric growth of organs of young larvae has been related to specific functions at given periods of a fish's life (Sala et al. 2005). Measurements of enzymatic activities in whole fish may reflect changes in the proportions of aerobic (digestive organs and nervous system) and anaerobic (muscles) tissues. Therefore, we measured digestive tracts (from oesophagus to anal opening) and livers of 57 individuals with weights ranging from 43.7 mg to 1.35 g, for comparison with the somatic weights. Wet and dry weights of digestive tract, liver, and somatic tissues were also recorded.

Tissue homogenization and enzyme assays

Whole fish were homogenized using a Polytron Tissue Tearor™ (Biospec Products Inc., Batlesville, Oklahoma; 3 × 10 periods at maximal speed) in 9 volumes of ice-cold Tris–HCl buffer (pH 7.5). A 150 µL volume of homogenate was centrifuged (15 min at 13 000*g*) for measurement of lipase and amylase, while a 250 µL volume was centrifuged at 3500*g* for 10 min for measurement of trypsin. Enzyme activities were determined in replicate samples, and all enzyme activities were measured at 15 °C, with the exception of amylase (37 °C). Trypsin (EC 3.4.21.4) and lipase (EC 3.1.1.34) were assayed using an F-2500 spectrofluorimeter (Hitachi Ltd.), while amylase (EC 3.2.1.1), citrate synthase (CS: EC 4.1.37), aspartate aminotransferase (AAT: EC 2.6.1.1), β-hydroxyacyl-CoA dehydrogenase (HOAD: EC 1.1.1.35), pyruvate kinase (PK: EC 2.7.1.40), lactate dehydrogenase (LDH: EC 1.1.1.27), and amylase (EC 3.2.1.1) were assayed using a UV–VIS spectrophotometer (Lambda 11, Perkin-Elmer). Both systems were equipped with a thermostated cell holder connected to a cooling water bath. Enzyme activities are presented in units per gram of fish (U·g fish^{-1}). Assay conditions for the enzymatic measurements were adapted from Lemieux et al. (2003).

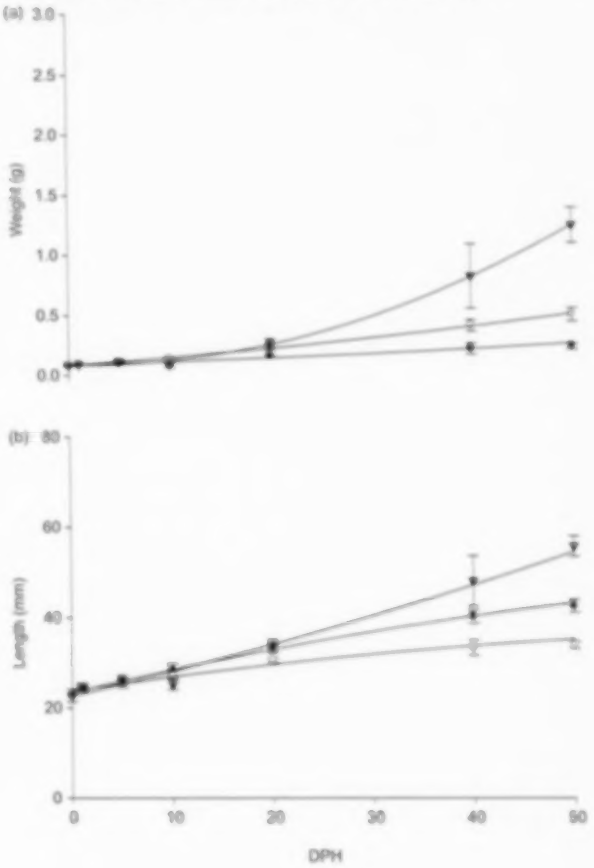
Protein analysis

Protein content was measured using the bicinchoninic acid method (Smith et al. 1985). All chemicals were obtained from Sigma Chemical (St. Louis, Missouri).

Statistical analysis

Results are presented as mean ± standard deviation. SYSTAT 10.2© (SYSTAT Software Inc., Point Richmond, California) was used for all statistical analyses. Nested analysis of variance (ANOVA) and the Tukey post hoc test were used to test differences among experimental groups. The relationships among enzyme activities, weight, and age of fish were tested by regression analysis and analysis of covariance (ANCOVA). The Bartlett χ^2 statistic was used to test if the correlation coefficient was significantly different from zero. We verified the normal distribution of residuals with the Kolgomorov–Smirnov test with the Lilliefors correction; some variables were log-transformed to normalize the distribution. Pearson's correlation were used to test the relations between digestive enzymes and corresponding metabolic enzymes. The strength of relationships between measured variables was investigated using principal component analysis (PCA).

Fig. 1. (*a*) Mean weight (g) and (*b*) length (mm) ± standard error of juvenile Atlantic wolffish (*Anarhichas lupus*) exposed to different feeding (solid circles, LA: maintenance *Artemia* ration; open circles, EA: excess *Artemia* concentration; triangles, FF: formulated feed) in relation to days after hatch (DPH).



Results

Mean weight and length on hatching day were 82 ± 4 mg and 22.7 ± 1 mm, respectively. There were no mortalities during the 50-day experimental period, even in the highly restricted LA group.

Growth rates during the 50-day exponential growth phase of the experiment differed according to type of feed and ration level (Fig. 1). Specific growth rates, in percent weight per day, were 1.27 ± 0.15, 0.52 ± 0.05, and 0.25 ± 0.02 in the FF, EA, and LA groups, respectively, and were significantly different (FF > EA > LA). In comparison with the *Artemia*-fed groups, there was a noticeable delay in growth of FF fish during the weaning period, probably related to the delay in feeding until general acceptance of the formulated feed. Thereafter, growth of FF fish increased, and the mean weight and length of these fish were significantly higher at the end of the experiment.

With the exception of lipase, HOAD, and amylase, enzyme activities were positively correlated with DPH (Table 1). Lipase and HOAD activity levels were related to DPH in the

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Table 1. Regression parameters of enzyme activities in relation to days after hatch (DPH) in groups of newly hatched Atlantic wolffish (*Anarhichas lupus*) fed excess *Artemia* (EA), a maintenance *Artemia* ration (LA), or a formulated feed (FF).

	LA			EA			FF		
Enzyme	Slope	Intercept	R^2	Slope	Intercept	R^2	Slope	Intercept	R^2
Lipase	3.016	210.53	0.13	—	—	—	—	—	—
HOAD	0.263	54.46	0.18	—	—	—	—	—	—
Amylase	—	—	—	—	—	—	5.039	279.86	0.25
PK	1.86b	435.15	0.10	3.50b	441.96	0.36	10.59a	416.39	0.60
Trypsin	0.03	1.99	0.51	0.02	1.69	0.45	0.03	1.87	0.47
AAT	2.43a	147.37	0.80	1.06b	150.15	0.53	1.67b	160.25	0.44
CS	0.59a	74.06	0.61	0.30ab	72.05	0.34	0.24b	77.60	0.35
LDH	3.33a	719.84	0.25	12.65b	726.72	0.64	31.59c	652.15	0.90

Note: Values with different letters indicate significant differences of slopes between groups ($P < 0.05$). HOAD, β-hydroxyacyl-CoA dehydrogenase; PK, pyruvate kinase; AAT, aspartate aminotransferase; CS, citrate synthase; LDH, lactate dehydrogenase.

Table 2. Regression parameters of enzyme activity in relation to weight (log, g) in groups of newly hatched Atlantic wolffish (*Anarhichas lupus*) fed excess *Artemia* (EA), a maintenance *Artemia* ration (LA), or a formulated feed (FF).

	LA			EA			FF		
Enzyme	Slope	Intercept	R^2	Slope	Intercept	R^2	Slope	Intercept	R^2
Lipase	149.78	565.4	0.18	—	—	—	—	—	—
HOAD	8.39	75.81	0.11	—	—	—	—	—	—
Amylase	—	—	—	—	—	—	96.98	518.79	0.31
PK	69.37b	606.59	0.08	91.07a	660.73	0.34	187.85a	894.05	0.63
Trypsin	1.01	4.47	0.42	0.55	3.06	0.35	0.55	3.25	0.50
AAT	95.58a	381.51	0.71	27.25b	215.97	0.49	28.06b	232.59	0.40
CS	23.02a	130.58	0.53	7.69b	90.65	0.31	4.49b	88.71	0.41
LDH	168.05c	1116.65	0.37	350.45b	1555.41	0.70	561.36a	2077.87	0.93

Note: Values with different letters indicate significant differences of slopes between groups ($P < 0.05$). HOAD, β-hydroxyacyl-CoA dehydrogenase; PK, pyruvate kinase; AAT, aspartate aminotransferase; CS, citrate synthase; LDH, lactate dehydrogenase.

highly restricted LA group, while the amylase activity showed a significant relation with DPH in the FF group only. The activities of PK, AAT, CS, and LDH varied with DPH, and all were affected by nutritional restriction (ANCOVA). The slopes of specific activities of AAT and CS were steeper for group LA than for group FF ($F_{[2,130]} = 10.28$, $P < 0.001$ and $F_{[2,106]} = 7.403$, $P = 0.001$ for AAT and CS, respectively), corresponding to 2.4- and 1.4-fold increases for AAT and CS, respectively. In contrast, slopes of PK and LDH activities were steeper for group FF than for group LA ($F_{[2,128]} = 22.222$, $P < 0.001$ and $F_{[2,131]} = 118.467$, $P < 0.001$ for PK and LDH, respectively, and increases of 5.6- and 9.5-fold for PK and LDH, respectively). Trypsin activity varied with DPH, yet there were no significant differences between groups. There were no differences in protein content (49.6 ± 8.2 mg·g fish^{-1}) between groups over the course of the experiment, and the same trends were observed when enzymes were expressed as U·mg protein^{-1} (results not shown).

Activities of lipase and HOAD in the LA group were only slightly correlated with weight, while amylase activity was correlated with weight only in the FF group (Table 2). Slopes of AAT and CS activities were steeper in the maintenance group LA compared with the unrestricted groups EA and FF (ANCOVA: AAT: $F_{[2,130]} = 22.577$, $P < 0.001$; approximately three times steeper slope in LA than in EA or FF; CS: $F_{[2,106]} = 16.769$, $P < 0.001$; three times and five times steeper slopes higher in LA than in EA or FF, respectively). Trypsin activity displayed a strong tendency (ANCOVA; $F_{[2,129]} = 2.894$, $P = 0.059$). Activities of PK and LDH presented an opposite relationship, with steeper slopes in the group FF than in the EA and LA groups (ANCOVA; $F_{[2,128]} = 6.932$, $P = 0.001$ and $F_{[2,131]} = 38.570$, $P < 0.001$, respectively). Only LDH presented significantly different slopes for every group (LA > EA > FF). When enzymes were expressed as U·mg protein^{-1}, the same trends were observed as with DPH (results not shown). The ratio of aerobic to anaerobic enzymes (CS/LDH) was negatively correlated with weight (log) and DPH and positively correlated with SGR in groups EA and FF. The CS/LDH ratio in the LA group was not correlated to SGR, weight, or DPH (not shown).

Aerobic metabolic enzymes AAT and glutamate dehydrogenase (GDH) showed strong correlations with trypsin activity in the LA group. Trypsin and AAT were also correlated in the EA group but not GDH, yet no significant relationships were detected in the FF group. However, the correlations of both PK and LDH with amylase were significant in the FF group, but not in the EA or LA groups (Table 3).

Collected data were subjected to a PCA (Fig. 2). The activities of GDH, HOAD, and amylase were only weakly correlated with SGR (Pearson's correlation coefficients of 0.1 to –0.1); these data were excluded to reduce the "noise" generated by weakly correlated variables. The analysis separated the data set into two principal components that

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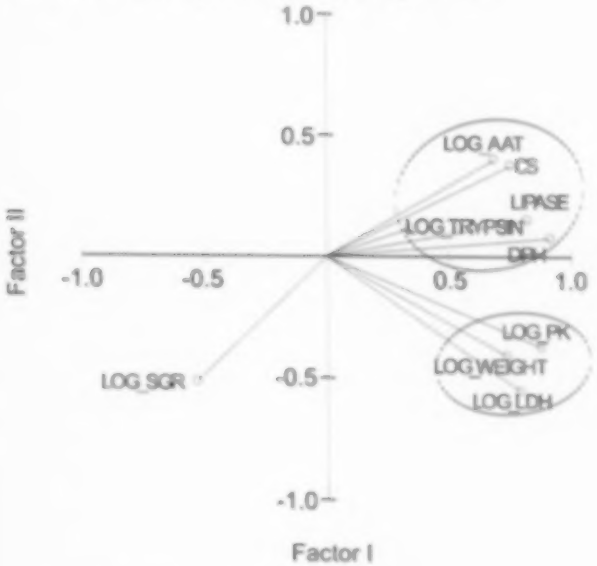
Table 3. Pearson's correlation coefficient of enzyme activities in relation to the associated digestive enzyme (AAT and GDH with log(trypsin); PK and log(LDH) with amylase).

		Pearson's *R*		
		LA	EA	FF
AAT	log(trypsin)	0.71	0.58	0.26
GDH	log(trypsin)	0.59	–0.04	0.02
PK	Amylase	0.02	0.19	0.48
log(LDH)	Amylase	0.19	0.17	0.62

Note: LA, a maintenance *Artemia* ration; EA, excess *Artemia* diet; FF, formulated feed; AAT, aspartate aminotransferase; GDH, glutamate dehydrogenase; PK, pyruvate kinase; LDH, lactate dehydrogenase.

Fig. 2. Position of the vector–variables in the plot of the first two principal components. AAT, aspartate aminotransferase; CS, citrate synthase; DPH, days after hatch; PK, pyruvate kinase; LDH, lactate dehydrogenase; SGR, specific growth rate.



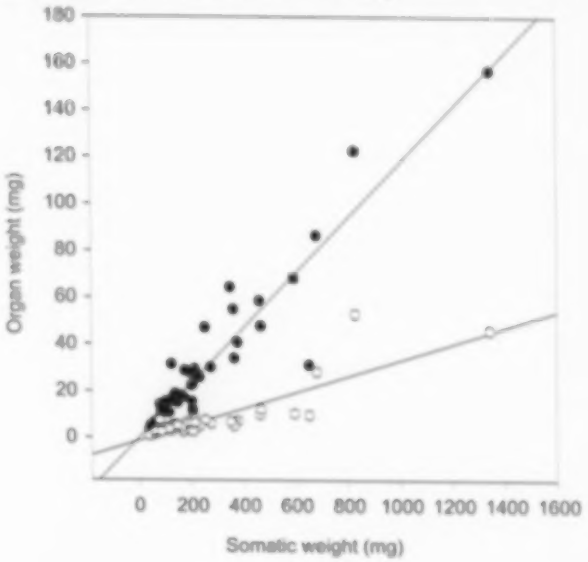
explained 54.33% and 13.57% of the variance in the data set. The first component separated SGR from the other variables because of the negative relation of SGR with DPH, while all other variables were positively related to DPH. The second principal component separated the data set into two clusters: one regrouping AAT, CS, trypsin, lipase, and DPH; the other regrouping PK, LDH, weight, and SGR.

Weights of digestive tract and liver scaled isometrically with fish weight. The corresponding regression equations are as follows: $W_{DT} = 0.117W_F - 0.126$ ($R^2 = 0.90$) and $W_L = 0.035W_F - 1.329$ ($R^2 = 0.75$), where W_{DT} is digestive tract weight, W_L is liver weight, and W_F is fish weight (mg) (Fig. 3).

Discussion

Good survival and growth after hatching is a function of the quality of eggs and larvae (Kjorsvik et al. 1990; Lamarre et al. 2004). Wolffishes are considered to be fully developed juveniles after hatching. Falk-Petersen and Hansen (2001 and 2003) described the development of the digestive system during the first free-living period of life of *A. lupus* and *A. minor* and concluded that the digestive organs of wolffishes at hatching appeared to be fully functional. Lamarre et al. (2004) reported that early growth and survival of newly hatched Atlantic wolffish was linked to levels of various digestive and metabolic enzymes. There was no mortality during these experiments, an indication of the quality of the wild egg masses as well as the larvae used for our growth trials. The known negative effects of poor egg and larval quality on digestive and metabolic enzymes activity were thus limited, allowing a clearer evaluation of the effects of feeding type or feeding level.

Fig. 3. Relationship of digestive tract (solid circles) and liver weight (open circles) with fish somatic weight.



The results of the PCA suggest the existence of two types of development for the main energetic metabolism pathways. The glycolytic enzymes PK and LDH are clearly linked to weight, as they are clustered in the fourth quadrant of the PCA. These enzymes are also related to specific growth rate, as they are found in the lower half of the plot. The aerobic enzymes AAT and CS, as well as digestive enzymes trypsin and lipase, are clustered in the first quadrant along with development time (expressed as DPH). Thus, the activities of these aerobic and digestive enzymes are associated with larval development time, while the expression of glycolytic enzymes is related to weight gain. These trends are confirmed by the regression analysis of enzyme activities in relation to weight and DPH. The slopes of the regression lines of AAT and CS in relation to weight are steeper for LA compared with EA and FF and significantly lower for LDH and PK. It has been previously shown that the glycolytic enzymes PK and LDH are positively associated with weight in wolffishes (Lamarre et al. 2004: *A. lupus*; Imsland et al. 2006: *A. minor*) and in other species (Somero and Childress 1980; Martinez et al. 2000). To our knowledge, this is the first observation of a discrepancy in the development of glycolytic, aerobic, and digestive enzymes.

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We verified that the relative weights of the liver and digestive tract were proportional to somatic weight in wolffish, as has been shown for *Cyprinus carpio* (Alami-Durante 1990) and *Pagrus major* (Oikawa et al. 1992). Hence, the trends of development described by the PCA and regression analyses are not artefacts of an allometric relationship between the aerobic organs (digestive and liver tissue) and the largely anaerobic tissues (i.e., muscle). A change in relative protein concentration during development could also be another confounding effect, as it is often observed in larval marine fish during metamorphosis (described by Zambonino-Infante and Cahu 2001). However, we found no significant relationships between protein content and age or weight of fish in any group (LA, EA, or FF) from hatching to 50 DPH (results not shown). The developmental trends observed in larval wolffish are thus clear evidence of differences in digestive and metabolic functions between the treatment groups and should be viewed as physiological events with a functional importance.

Our results clearly demonstrate that feeding conditions modulate the developmental pattern of enzyme activities, similar to the findings of Segner and Verreth (1995). The activities of lipase, HOAD, AAT, CS, and to some extent trypsin are increased under food restriction conditions, whereas those of PK, LDH, and amylase are increased when food supply is sufficient (in quality and quantity). Food-restricted fish, or fish re-fed after a period of starvation, display a similar mechanism (i.e., increases in CS activity (Bélanger et al. 2002) and the catabolism of amino acids (Mendez and Wieser 1993; Segner and Verreth 1995)) before the animals resume growth and an increased glycolytic metabolism. The increased activity of aerobic (AAT, CS, and HOAD) and digestive (trypsin and lipase) enzymes seem coordinated and given precedence under conditions of food restriction. This strategy may permit the animal to resume growth and regain an optimal physiological state when food supply is reestablished following a period of starvation. The relatively high levels of activity may also be a response enabling fish to process internal energy reserves (adipose and protein) when food supply is limited or scarce.

The significant relationships among amylase activity, weight, and DPH in group FF might be related to the higher levels of carbohydrate in formulated feed, as suggested by Pérez et al. (1996), Ribeiro et al. (2002), and Mohapatra et al. (2003). These workers reported increases in levels of amylase activity when fish of different species (*Dicentrarchus labrax*, *Solea seleganensis*, and *Labeo rohita*, respectively) were fed formulated diets. Many species, including haddock (*Melanogrammus aeglefinus*), Atlantic cod (*Gadus morhua*) (Perez-Casanova et al. 2006), and Arctic char (*Salvelinus alpinus*) (Lemieux et al. 2003) have a limited ability to digest carbohydrates after hatching. Zambonino-Infante and Cahu (2001) reported that amylase activities in sea bass (*Dicentrarchus labrax*) and red drum (*Sciaenops ocellatus*) decrease after the third week after hatch. In contrast, wolffishes demonstrate a good capacity to digest carbohydrates from hatching. In this study, amylase activity levels in Atlantic wolffish averaged 6.6 ± 3 U·mg protein^{-1} on the first day after hatch and increased in the FF group during the 50 days of the experiment. These levels of activity are much higher than those found in Arctic char, where activities assayed by the same method gave results below 1 U·mg protein^{-1} (H. Lemieux, unpublished data) and showed no relation with DPH (Lemieux et al. 2003).

It has been suggested that growth may be limited by digestive processes (Blier et al. 1997). To sustain higher growth rates during compensatory growth, the expression of digestive enzymes, such as trypsin, may be fuelled by ATP from the activity of oxidative metabolism enzymes, such as AAT, HOAD, and CS. Higher glycolytic capacities in rapidly growing fish have been reported in many studies (Pelletier et al. 1994; Segner and Verreth 1995; Imsland et al. 2006). It has been suggested that once food becomes available, the correlation between glycolytic enzymes and growth rate facilitates the maintenance of good swimming capacity and aggressive behaviour once food becomes available (Le François et al. 2005). The persistence of a catabolic capacity and the uncoupling of glycolytic and aerobic metabolism enzymes during periods of food restriction may be an adaptative mechanism that ensures that the food-restricted fish can maintain a relatively high metabolism and rapidly resume growth upon refeeding. All three mechanisms could ensure the preservation of a competitive advantage in adverse conditions.

The relationships among age, weight, growth rate, and enzyme activity in fish are complex. The large sizes of wolffish eggs and larvae in combination with the use of highly sensitive microassays allow several enzymes to be assay in a single individual, thus permitting a more precise evaluation of the relationship between different enzymes and pathways. However, a limitation of this approach is that it is not possible to distinguish activities in different organs (liver, muscle, gills, etc.), since enzyme activities are measured in whole larvae. This study proposes two nonexclusive explanations of the physiological significance of the relationships we observed: (*i*) aerobic enzyme activities are maintained at a level sufficient to efficiently metabolize the exogenous and endogenous energy reserves during a period of food restriction, and (*ii*) muscle tissues are reorganized from aerobic to glycolytic fibres in fast-growing juveniles. To distinguish between these two mechanisms, more work should be done on specific tissues (e.g., digestive organs and muscle) of newly hatched wolffish given different types and rations of food. Finally, the use of wolffish juveniles as a model species is clearly warranted because of their size and advanced developmental stage at hatching.

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Population genetic structure in the North Atlantic Greenland halibut (*Reinhardtius hippoglossoides*): influenced by oceanic current systems?

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Abstract: We report statistically significant genetic structure among samples of Greenland halibut (*Reinhardtius hippoglossoides*), rejecting the null hypothesis of panmixia in the North Atlantic. The species appears instead to be subdivided into partially isolated populations, with some evidence for isolation by distance. However, there is a dichotomy between transatlantic sample comparisons and those within a regional current system, even when geographic distance is similar. Calculating geographic distance along the flow of ocean currents gave a more linear correlation with genetic differentiation than straight-line geographic distances, suggesting that gene flow follows ocean currents. We hypothesize that gene flow is mediated by drift of eggs and larvae with ocean currents, a hypothesis that is consistent with the extended pelagic phase of Greenland halibut larvae. This implies an important role for ocean currents in shaping the genetic structure of this and potentially other deep-sea species.

Résumé : Nous signalons l'existence d'une structure génétique significative dans des échantillons du flétan du Groenland (*Reinhardtius hippoglossoides*) et nous rejetons donc l'hypothèse nulle de panmixie dans l'Atlantique Nord. L'espèce semble plutôt subdivisée en populations partiellement isolées, avec des indications d'un isolement par distance. Il y a cependant une dichotomie entre les comparaisons faites entre les échantillons récoltés en travers de l'Atlantique et entre ceux qui appartiennent à un système de courants régionaux, même lorsque les distances géographiques sont semblables. Le calcul des distances géographiques le long du parcours des courants océaniques donne une corrélation plus linéaire avec la différenciation génétique que les distances géographiques en ligne droite, ce qui indique que le flux génétique suit les courants océaniques. Nous émettons l'hypothèse selon laquelle le flux génétique est géré par la dérive des oeufs et des larves dans les courants océaniques, une hypothèse qui est compatible avec la phase pélagique prolongée des larves du flétan du Groenland. Notre étude reconnaît un rôle important aux courants océaniques dans l'élaboration de la structure génétique chez cette espèce et potentiellement chez d'autres espèces marines des eaux profondes.

[Traduit par la Rédaction]

Introduction

Abundant, highly mobile species with a large effective population size could be expected to show panmixia over a broad geographic range, perhaps across the species range. In the marine environment, there are many species that fall into this category, given the lack of obvious boundaries to gene flow in open water. However, many such species do show population genetic structure (see review in Graves 1995; Knutsen et al. 2003, 2004). Further, the depletion of these species is an important concern (e.g., see Devine et al. 2006), especially when cryptic population structure is unrecognized and therefore cannot be incorporated into effective conservation strategies. Here, we investigate the mechanisms that may underlie the evolution of population structure for many oceanic species in the North Atlantic, using Greenland halibut (*Reinhardtius hippoglossoides*) as an example.

Greenland halibut is distributed in Arctic and boreal waters on both sides of the North Atlantic (Fedorov 1971). The stocks support important fisheries in comparatively deep waters outside Canada, Greenland, Iceland, Faroe Islands, and Norway (Godø and Haug 1989; Bowering and Brodie 1995). Greenland halibut, together with many deep-water species (Devine et al. 2006), is heavily exploited, and increasing fishing pressure is reinforcing the need for accurate data on stock structure. In the North Atlantic, Greenland halibut is

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presently perceived as consisting of three major stocks: the Northeast Arctic stock in the Barents Sea – Svalbard region; the West Nordic stock at Iceland, East Greenland, and Faroe Islands; and the Newfoundland – Baffin Bay – West Greenland stock complex (Boje 2002*a*). These stocks form the basis for the management of this species (ICES 2005*a*, 2005*b*; Darby et al. 2004). For all three stocks, potential spawning grounds, nursery areas, and feeding areas have been identified (Sigurðsson 1977; Godø and Haug 1989; Bowering and Brodie 1995). Nevertheless, the genetic studies that have been carried out to date have all failed to detect any differentiation within the North Atlantic (Riget et al. 1992; Vis et al. 1997; Igland and Nævdal 2001), with the exception of West Greenland and the Gulf of St. Lawrence, which appear genetically distinct from the remainder of the North Atlantic (Fairbairn 1981; Riget et al. 1992).

The Greenland halibut generally prefer depths of 200–800 m (Fedorov 1971), but may extend down to 1500–1800 m in some areas (Bowering and Brodie 1995). During spawning, the depth preference is more limited (600–900 m; Fedorov 1971). The species aggregate during a main spawning season, but may also spawn far outside such spatial and temporal limits (Albert 2003; Albert et al. 2001*a*; Bowering and Brodie 1995). Eggs and larvae remain pelagic for several months, which is needed both for the development of the larvae and for the larvae to reach the nursery areas.

Ocean currents are believed to carry spawning products from the spawning grounds to the nursery areas (see Godø and Haug 1989; Boje 2002*a*). At the spawning ground in the Davis Strait, currents may carry pelagic larvae either north (by the West Greenland Current) to Baffin Island or south (by the Labrador Current) to Labrador or Newfoundland. Likewise, eggs and larvae spawned along the continental slope off the Norwegian coast (66°N–75°N) are probably transported north to Svalbard by the Svalbard Atlantic Current (Godø and Haug 1989). Simulations with drift models have confirmed that the areas north and northeast of Svalbard are likely to be important nursery areas for Greenland halibut (Ådlandsvik et al. 2004). Spawning grounds west of Iceland span over great areas (Sigurðsson 1979), and modeling has shown that eggs and larvae could be retained within the area between Iceland and Greenland or, alternatively, transported around Cape Farewell towards the west coast of Greenland, depending on the exact spawning location (Boje 2002*a*). Larvae may also drift with ocean currents from the Northeast Arctic towards East Greenland, possibly connecting the Northeast Arctic stock, pragmatically defined as the entity exploited in the Barents Sea and adjacent slope areas, with the presumed West Nordic stock (Albert et al. 2001*b*; Ådlandsvik et al. 2004). Migration of adult individuals may also serve as links between the presumed stocks, and tagging studies have, for instance, demonstrated migration from Iceland to the Barents Sea (Sigurðsson 1981; Boje 2002*a*, 2002*b*).

The great potential for migration and passive transport by ocean currents in this species is expected to result in gene flow among presumed stocks, which may lead to genetic homogenization over large geographic areas. Such gene flow may explain the apparent lack of genetic structure in Greenland halibut within the North Atlantic (Vis et al. 1997; Igland and Nævdal 2001). However, although transport of pelagic eggs and larvae by current systems may lead to extensive gene flow (Stenseth et al. 2006), current systems could also act as retention systems and barriers to gene flow, as have been observed in, for example, Atlantic cod (*Gadus morhua*) in the large North Atlantic banks (Anderson 1982; Page et al. 1999; Ruzzante et al. 2001). Such retention systems may possibly explain the observed genetic differentiation in Greenland halibut along West Greenland and the Gulf of St. Lawrence (Fairbairn 1981; Riget et al. 1992), as well as indirect evidence for stock structure observed in the prevalence of parasites (Boje et al. 1997) and in geographical differences in the mean number of vertebrae (Riget et al. 1992).

Here, we test the hypothesis that oceanographic systems are important in shaping the genetic structure of this species through the distribution of pelagic eggs and larvae by currents. This hypothesis predicts discordance between a simple isolation by distance model and the observed pattern of differentiation. We combine high-resolution genetic analysis with a sampling strategy that provides sufficient power to test for differentiation in the context of both geographic distance and oceanic current systems and reveal a pattern of structure that suggests a major role for large-scale current systems.

Materials and methods

The study area covers the larger part of the species' distribution range in the North Atlantic (Fig. 1). About 100 individuals from each of six localities were sampled with trawl in 2004 (Table 1; the sample from East Greenland was taken by longline). The Svalbard sample consists of bottom-settled juvenile individuals (average size 17.25 cm), whereas all other samples consist of a mixture of mature and immature adults. In addition, we included two earlier (2001) samples from Baffin Bay ($n = 41$) and Davis Strait ($n = 20$), combined into a single sample denoted "Canada" (cf. Fig. 1, Table 1). This pooling, which was suggested by the apparent lack of genetic heterogeneity between the two sites (exact test for allele frequency heterogeneity: p value = 0.37), was done to increase the sample size and improve statistical power in subsequent statistical analyses. All sampled fish were sexed, weighed, measured, and assigned to a sexual maturity index (according to Fotland et al. 2000). Samples of white skeletal muscle were taken from fresh specimens and stored in 96% ethanol until DNA extraction.

DNA was isolated from muscle tissue using a commercial extraction kit (Qiagen, Inc.). Nine polymorphic microsatellite loci previously developed for a related species (Atlantic halibut, *Hippoglossus hippoglossus*) were amplified with polymerase chain reaction (PCR), following published protocols or slight modifications thereof: HhiA44, HhiC17, and HhiI29 (McGowan and Reith 1999); Hhi1, Hhi3, Hhi52, Hhi53, Hhi55, and Hhi59 (Coughlan et al. 2000). Microsatellite fragments were separated and scored on ALFexpress II automatic DNA analyzers (Amersham Pharmacia Biotech). Care was taken to avoid misclassification of alleles and genotypes during scorings, and different manufactures of *Taq* polymerase – PCR amplification buffers and different PCR conditions were explored to reduce short allele dominance. The loci Hhi1 and Hhi55

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Fig. 1. Map of sample localities (solid circles). Black arrows indicate the main currents, whereas the red dotted line shows the downstream current distance used in the analysis. Dark colors indicate deep zones and brighter colors shallow waters, as indicated in the legend.

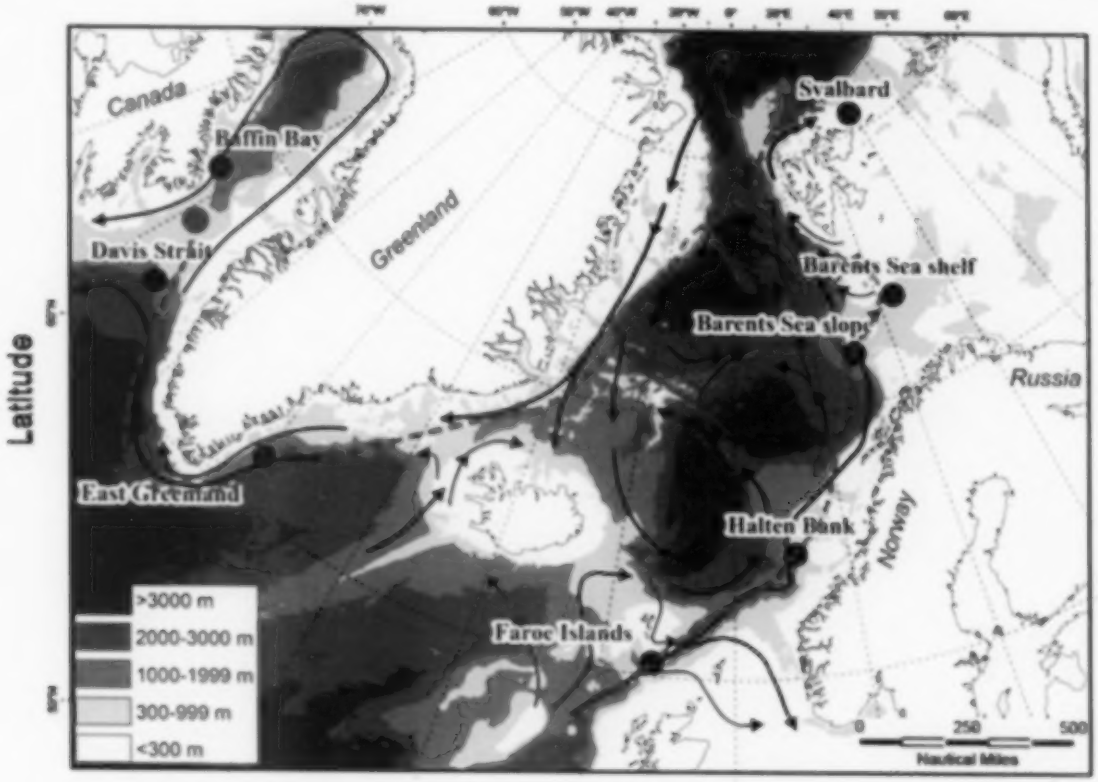

Table 1. Samples of Greenland halibut (*Reinhardtius hippoglossoides*) for genetic analyses.

Sampling location	Abbrev.	Date	Depth (m)	Sample size*	Percentage mature†	Average size (cm)	Spawning area?
Faroe Islands	FI	June 2004	460	97	35	56.3	Unknown
Halten Bank	HB	March 2004	657	100	28	58.5	Unknown
Barents Sea Slope	BL	Dec. 2004	909	93	80	54.2	Yes
Barents Sea Shelf	BH	March 2004	473	93	62	52.9	Unknown
East Greenland	GR	June 2004	1170	100	87	70.6	Unknown
Canada	CA	Nov. 2003	1224–1365	61	NA	56.6	Unknown
Svalbard	SV	Sept. 2004	564	95	0	17.3	Nursery area

Note: Samples were not from any known spawning concentrations or nursery areas, apart from the BL and SV samples.
*Sample size excludes a total of 17 individuals with poor DNA quality. See text for details.
†Mature individuals are either maturing (thought to spawn in next spawning season) or spawning (maturity index 2–4). For CA, maturity indexes were not available.

were difficult to score, because of stutter bands (Hhi1) and allele competition during PCR (Hhi55), and numerous reruns were performed to ensure that they were scored consistently. All tentative homozygotes were re-amplified and screened a second time to minimize misclassification of heterozygotes. Two people independently scored all genotypes.

Amounts of genetic variation within samples were characterized by the observed (H_O) and expected (H_E) heterozygosities and by allele richness at each locus separately. An estimate of the average variability in the total material (H_T) was calculated according to Nei and Chesser (1983). Deviations from Hardy–Weinberg genotype proportions within loci were estimated by F_{IS}, and deficiencies and excesses of heterozygotes were tested for separately using one-sided exact tests in the software GENEPOP (Raymond and Rousset 1995).

Genetic differences among localities were estimated with F_{ST} using Weir and Cockerham's (1984) estimator θ, both over all samples and between pairs of samples. The statistical significance of genetic differences was evaluated by

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means of exact tests using GENEPOP software with 100 000 replicates. The tests were carried out on each locus separately, and the p values from the single-locus tests were combined into joint tests for genetic differentiation with Fisher's summation procedure, as recommended by Ryman and Jorde (2001). To provide further comparative assessment of possible population structure, genetic distances (D_A: Nei et al. 1983) were calculated among samples and visualized by multidimensional scaling (MDS) using XLStat (Addinsoft), and an assignment test was performed using a Bayesian approach in GENECLASS 2.0 software (Piry et al. 2004) with the option "self-classification of reference data" (Rannala and Mountain 1997). We assigned the juvenile individuals from Svalbard to each of the adult samples, using the same software as a test for the most likely population source for these juveniles.

We tested for geographic patterns of genetic differentiation by regressing genetic differentiation against geographic distance between pairs of samples, following Rousset (1997). Two different tests were carried out to account for different hypotheses of gene flow: adult dispersal in two-dimensional space and unidirectional (one-dimensional) transport of pelagic larvae by ocean currents (cf. Fig. 1). In the first case, pairwise $F_{ST}/(1 - F_{ST})$ values were regressed against the natural logarithm of geographic distance, using the shortest (straight line) map distance. Log-transformed distances were used because the sampled area represents a two-dimensional habitat for adult Greenland halibut and, under the assumption of isolation by distance, a linear relationship between $F_{ST}/(1 - F_{ST})$ and logarithmic (ln) distance is expected to evolve (Rousset 1997). In the second case, we measured the shortest downstream distance connecting samples, following the predominant ocean currents (along the red dotted line in Fig. 1) from the Faroe Island to the Barents Sea, with a separate curl over to north of Svalbard and another meeting the Arctic Current on its southward path along East Greenland, and finally looping into the Davis Strait (we used a position in-between the two samples sites at Davis Strait and Baffin Bay, cf. red circle in Fig. 1). The downstream distances calculated along this path were used in a regression analysis of $F_{ST}/(1 - F_{ST})$ as before. This time we did not log-transform distances because the potential migration path along the current is essentially one-dimensional, and untransformed distances are therefore appropriate (Rousset 1997). For both distance measures, we used reduced major axis regression to estimate the regression of $F_{ST}/(1 - F_{ST})$ on distance, using IBDWS software (version 3.03; Jensen et al. 2005). Mantel tests were used to test the null hypothesis of no relationship between $F_{ST}/(1 - F_{ST})$ and distance.

Because of the relatively low level of genetic differentiation in this species, there is the possibility of nonrandom sampling biasing the estimated F_{ST} (Waples 1998). Ideally, temporal replicates from the same sample localities may be included to check on the consistency and temporal persistence of the observed structure. For deepwater fishes, like the Greenland halibut, it is impractical and expensive to collect replicate samples. We instead used available length data as a proxy for age classes and tested for the relative effects of age class (i.e., length) and stream distance on genetic differences among individuals. Using Rousset's (2000) measure of genetic differences within pairs of individuals, a_{ij}, we apply the following additive model to the adult samples (i.e., excluding the juvenile Svalbard sample):

$$a_{ij} \sim m_{ij} + d_{ij} + (m{:}d)_{ij}$$

where m_{ij} is the mean size (length) of two individuals, i and j; d_{ij} is the downstream distance between them; and $m{:}d$ is the interaction term between m and d. This latter term is included because there are length differences among samples (cf. Table 1) that may otherwise confound the analysis. We used the generalized linear model (GLM) function in the R statistics package (R Development Core Team 2006) to calculate the effects of the factors m, d, and $m{:}d$ on a, with the number of simultaneously scored loci in the two individuals as weights. Because the data consist of paired measures, conventional assumptions of independence among measurements cannot be made, and we used permutation techniques to test the significance of each factor. The permutation test was performed by repeatedly (20 000 times) randomizing length and geographic position among individuals, while leaving genotypes as observed and calculating the effects of the randomized lengths and positions. The fraction of replicates that yielded a larger effect on a factor than that observed in the real (unperturbed) data was taken as the p value for the effect of that factor on genetic difference, a.

Results

Our results are based on 639 individual Greenland halibut that could be reliably scored at all or most of the nine microsatellite loci. These exclude 17 individuals that could not be scored at four or more loci and that therefore were judged as having poor DNA quality.

There are large differences in the amount of genetic variability among loci; the overall heterozygosity, H_T, ranges from 0.043 at locus Hhl52 to 0.961 at locus Hhl29, and the number of alleles range from 2 at Hhl52 to 61 at Hhl53. All samples conform to Hardy–Weinberg genotype proportions at six loci, whereas the three loci Hhl1, Hhl53, and Hhl55 consistently display heterozygote deficiency in every sample (Appendix A). Individuals with missing values at any of these three loci typically lack only one of these genotypes and were successfully scored at the remaining loci. This suggests that poor sample quality (as noted above) was not the cause for the heterozygote deficiencies at these three loci and that segregation of nonreplicated or "null" alleles may be a more likely explanation. Null alleles at Hhl1, Hhl53, and Hhl55 are indeed reported by the MICRO-CHECKER software (van Oosterhout et al. 2004), with average frequencies within samples of 0.16 at Hhl1, 0.09 at Hhl53, and 0.21 at Hhl55 (Appendix A). The existence of null alleles is not surprising considering that the primers were developed for a different species (Atlantic halibut), which increases the possibility of mutations occurring in the primer regions (Pemberton et al. 1995). The hypothesized null alleles appear rather uniformly distributed among samples (cf. Appendix A) and need not represent a problem for the analysis of population structure. To be on the safe side, we carry out all statistical analyses on the remaining six loci while, for comparison, also report results of tests that include the potentially problematic loci Hhl1, Hhl53, and Hhl55.

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Table 2. F_{ST} values between pairs of samples (averaged over six loci below diagonal and over nine loci above diagonal) and joint exact tests for allele frequency heterogeneity over six (below diagonal) or nine (above diagonal) loci.

	FI	HB	BL	BH	GR	CA	SV (juveniles)
FI	—	–0.0001	0.0008*	0.0001*	0.0020*	0.0043*	0.0001*
HB	0.0004	—	0.0010	–0.0003	0.0004	0.0071***	0.0002
BL	–0.0002	–0.0009	—	–0.0001*	0.0028*	0.0099***	–0.0008
BH	–0.0005*	–0.00010	–0.0008	—	0.0014*	0.0087***	–0.0003***
GR	0.0030**	0.0002	0.0011***	0.0026*	—	0.0046*	0.0015***
CA	0.0034*	0.0024*	0.0072***	0.0071**	0.0042*	—	0.0050***
SV (juveniles)	–0.0011*	–0.0015	–0.0005	–0.0002	0.0003	0.0011*	—

Note: Some comparisons with slightly negative average F_{ST} estimates nevertheless come out as significant (with asterisks) in the exact tests. This reflects differences in how the two tests treat the data. For Fisher's summation procedure, asterisks denote level of significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. See Table 1 for location abbreviations.

The amount of genetic variability within sites, as judged by average heterozygosity (H_O) and average number of alleles per locus (A), is very similar among the sampled localities (Appendix A). However, a statistically significant fraction of the microsatellite variability is ascribed to differences among localities, $F_{ST} = 0.0018$, and the joint null hypothesis of no allele frequency differences among localities was rejected with high probability ($p < 0.0001$). The overall genetic differentiation remains significant after excluding the three potentially problematic loci (based on six loci: $F_{ST} = 0.0010$; $p < 0.05$), though losing three loci clearly reduces the power.

When comparing pairs of samples of Greenland halibut, the many sampled localities appear to be genetically differentiated from each other (9 out of the 21 pairwise tests were significant based on six loci, while 13 pairs were significant when basing the test on all nine loci; Table 2). The notable exception to the general observation of genetic differentiation refers to the sample from the Halten Bank, which differed significantly only from the sample from Canada. Also, the samples from Barent Sea Slope, Halten Bank, and Svalbard (cf. Fig. 1) were genetically very similar, thus contributing to the low overall F_{ST} (above). Most other pairs appear to be genetically differentiated from each other.

There is a clear tendency for genetic differentiation to increase with geographic distance, and the regression of pairwise $F_{ST}/(1 - F_{ST})$ values against log distance comes out highly significant based on the Mantel test (9 loci: slope 5.27×10^{-3}, $R^2 = 0.301$, $p = 0.001$; 6 loci: slope 3.94×10^{-3}, $R^2 = 0.208$, $p = 0.03$). Roughly, there seems to be little genetic differentiation among samples situated less than approximately 1000 km apart, whereas most pairs separated by greater distances are genetically differentiated (Fig. 2*a*). Although we fit a linear regression based on model expectations, the observed pattern clearly does not correspond to those expectations. Instead, there appears to be a threshold distance at approximately log distance 8 (about 3000 km), beyond which the highest F_{ST} values occur. The threshold refers to comparisons involving samples situated on different sides of the Atlantic, possibly indicating a separation into distinct East and West Atlantic populations or groups of populations. A stronger linear pattern emerges, however, when we replace log geographic distance with the downstream distance (Fig. 2*b*; 9 loci: slope = 1.77×10^{-6}, $R^2 = 0.500$, $p = 0.02$; 6 loci: slope = 1.32×10^{-6}, $R^2 = 0.433$, $p = 0.014$). As is evident from comparisons between Figs. 2*a* and 2*b*, genetic differentiation more clearly displays a linear relationship with downstream distances than it does with log geographic distances (or untransformed geographic distances; data not shown).

The results of the individual-based GLM model confirm the finding of (stream) distance having a significant effect on genetic differentiation (Table 3). The effect, which is significant when the three problematic loci are omitted, is positive and demonstrates that genetic differences increase with downstream distance (9 loci: $p = 0.06$; 6 loci: $p = 0.05$). There is, however, a nearly significant ($p = 0.06$), negative interaction effect of size and distance, $m{:}d$, on genetic differences. This negative interaction implies that the effect of stream distance may be weaker for large fish than for smaller ones. Alternatively, it may arise as a sampling effect because large fish are not randomly distributed among sample localities. Finally, the size of the fish (factor m) alone has little explanatory power for genetic differentiation among Greenland halibut, and the effect of size was far from significant (cf. Table 3). Hence, there is no evidence for size- or age-related (temporal) effects that could confound the analysis of spatial differentiation, and the observed geographic pattern appears temporally robust to the extent that can be judged from the available data.

An MDS plot of Nei's genetic distance, D_A (Fig. 3), provides further insights into the spatial genetic structure of the Greenland halibut. The analysis was performed separately with six and nine loci, with very similar results, and here we present the analysis with six loci only. The two first dimensions, together explaining 60% of the variability in genetic distance, separate all samples without much evidence for clustering or grouping of samples. Rather, the samples appear situated in rough agreement with their relative geographic positions (cf. Fig. 1). In particular, the ordering of the samples in this plot is consistent with the ordering encountered by the ocean currents, starting at lower right at Faroe Island and following a counter-clockwise arc through the diagram towards the Western Atlantic samples (East Greenland and Canada).

The assignment tests demonstrate highest assignment to the location of sampling for all adults (Table 4; diagonal values) and support the above findings of genetic structure in Greenland halibut. We note, however, that large proportions of individuals sampled at the Barents Sea Slope (26%) and at the Halten Bank (23%) assign to the Barents Sea Shelf. This indicates limited genetic structuring within the North-

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Fig. 2. Scatterplot and reduced major axis regression (solid line) of genetic differentiation, $F_{ST}/(1 - F_{ST})$, averaged over six loci, against distance between samples. Square symbols represent sample pairs on the same side of the Atlantic Ocean and circles represent transatlantic comparisons. Open symbols are used for pairs that include the Svalbard sample of juvenile fish. Distances are calculated in two different ways: (*a*) using ln-transformed linear (great circle) distances among all sample pairs(including Svalbard: solid line): slope = 3.94×10^{-3}; $p = 0.03$ (Mantel test), or just among the six adult samples (dotted line): slope = 3.9×10^{-3}; $p = 0.016$. (*b*) using minimum downstream distance among all sample pairs (solid line): slope = 1.32×10^{-6}; $p = 0.014$, or among adult samples (dotted line): slope = 1.27×10^{-6}; $p = 0.026$).

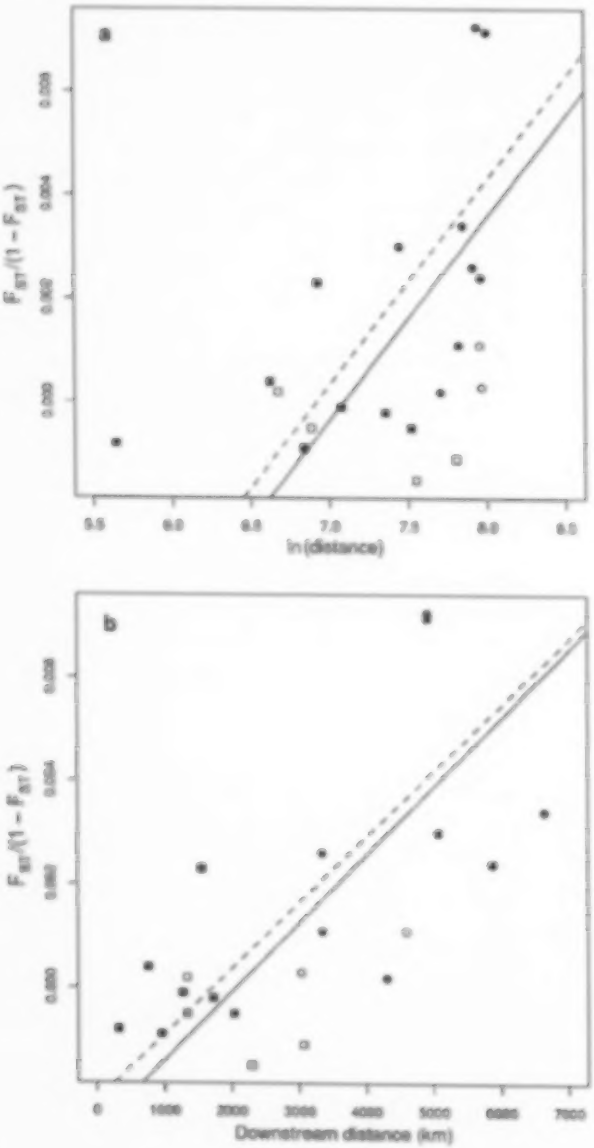
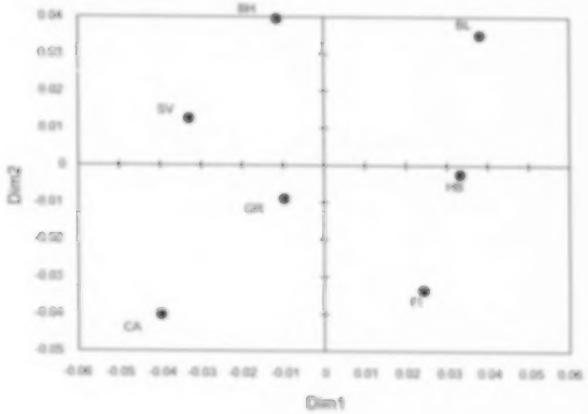


Table 3. Results of the generalized linear model (GLM) testing for effects of stream distance (*d*) and a proxy for age (mean length, *m*), and their interaction (*m*:*d*) on genetic difference between individuals.

	6 loci		9 loci	
Source	Estimate	*p*	Estimate	*p*
m	–0.002 58	0.24	–0.001 146	0.33
d	0.000 077	0.05	0.000 054	0.06
m:*d*	–0.000 001	0.06	–0.000 000 8	0.06

Note: Results are presented separately for genetic difference measured over all nine loci and over the six loci that did not segregate for null alleles. The *p* values are estimated from 20 000 replicated random permutations of data.

Fig. 3. Patterns of geographic structure in Greenland halibut (*Reinhardtius hippoglossoides*) revealed multidimensional scaling (MDS) of the matrix of genetic distances (D_A; Nei et al. 1983; Kruskal's stress = 0.241). The first axis may represent gradients along the currents (explaining 31% of the variation) and the second axis additional differences across the North Atlantic (explaining 29% of the variation).



east Atlantic (i.e., the Halten Bank and the Barents Sea Slope and Shelf), in accordance with the findings of the pairwise F_{ST} (cf. Table 2).

The assignment of juvenile Greenland halibut from Svalbard found that most of them assigned to adults from the nearby Barents Sea Shelf (29%) and Halten Bank (24%). Tentatively lumping the three Northeast Atlantic adult samples into a single group, because of their high cross-assignment (above; Table 4), results in an overwhelming large percentage (90%; see Table 4) of Svalbard juveniles assigning to this group. This supports the notion that the juveniles caught off Svalbard have their origin upstream somewhere from the Halten Bank to the Barents Sea.

Discussion

We found statistically significant genetic structure among samples of Greenland halibut, clearly rejecting the null hypothesis of panmixia in the North Atlantic, with differentiation generally increasing with distance between samples. Although the magnitude of F_{ST} differences were small, they were corroborated using very different methods (likelihood

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Table 4. The percentage of individuals assigned (i.e., having the highest likelihood) to each of the sampled populations calculated from multilocus genotypes (six loci; excluding the three loci with null alleles) using the GENECLASS 2.0 software.

	FI	HB	BH	BL	GR	CA
FI	**45**	7	24	7	10	7
HB	12	**39**	23	11	9	6
BH	13	12	**55**	8	10	2
BL	15	12	26	**28**	15	4
GR	14	15	17	1	**48**	5
CA	11	15	11	5	15	**43**
NEA (adults)*	6		(90)†		3	1
SV (juveniles)	20	24	31	9	13	3

Note: The last row gives the assignment of the juvenile sample from Svalbard (SV) to the adult samples. Data in bold represent the percentage of self-assignment. See Table 1 for location abbreviations.

*Northeast Atlantic.

†Pooling samples from the Halten Bank (HB), Barents Sea Shelf (BH), and Barents Sea Slope (BL).

assignments and multidimensional scaling) and are therefore unlikely to be simply due to noise. Further, a likely source of noise (temporal variation) was tested and excluded from being an important factor. The largest distances, whether measured along the shortest straight lines connecting the samples or along the ocean currents, refer to transatlantic pairs, and these pairs are also the most genetically divergent (average pairwise F_{ST} = 0.0028 for transatlantic pairs). The sample from Canada (combining subsamples from Baffin Bay and Davis Strait), in particular, is clearly the most divergent from other North Atlantic samples. This observation is in accordance with those of Riget et al. (1992), who reported genetic differentiation between a sample from Denmark Strait (localized between Greenland and Iceland) and samples from Newfoundland and West Greenland. Vis et al. (1997), on the other hand, did not detect any geographic differences in mtDNA haplotype frequencies. Studies on meristics did not reveal significant differences throughout the range either (Misra and Bowering 1984). However, tagging studies typically show high fidelity of Greenland halibut, with 90%–99% of tagged individuals remaining within the site of release in some offshore–inshore areas, and detect very few long-distance migrations (1100–2500 km) (Boje 2002*a*). This high degree of fidelity is in accordance with our findings of population structure in this species. Also, studies on parasite prevalence (Boje et al. 1997) demonstrate clear differences between each side of Greenland and also in the fjords of West Greenland. Similarly, Khan et al. (1982) and Arthur and Albert (1993) found differences in parasite infestations among Hamilton Bank, Newfoundland, Labrador, and north of Grand Bank. Such differences in parasite prevalence among Greenland halibut samples add support to the notion of stock structure, at least in the Northwest Atlanthe North Altantic (i.e., Canada excluded), and this has not been reported previously. Neither Igland and Nævdal (2001), whotic (Boje et al. 1997).

We also find genetic differences within the remainder of studied samples with a similar geographic distribution to the present study, nor Vis et al. (1997) found any statistically significant differentiation within this area. While statistical power is a complex function of degree of differentiation, amount of variability (number of alleles and heterozygosity), sample sizes, number of loci (Ryman et al. 2006; Waples and Gaggiotti 2006), the set of six (or nine) microsatellites, and large sample sizes employed in our study most likely provides increased power relative to studies based exclusively on mtDNA (Vis et al. 1997) or allozymes (Igland and Nævdal 2001).

While the general trend in our data is an increase in genetic differentiation with distance, the pattern is clearly not linear with linear distance or with log-transformed linear distance. Contrary to what is typically observed or expected theoretically in nonequilibrium situations (Slatkin 1993; Jorde et al. 2006), genetic differentiation does not taper off at large distances but instead increases rather abruptly. A possible explanation for this pattern is that there are two genetically different populations of North Atlantic Greenland halibut, one on each side of the Atlantic. Distant (transatlantic) sample pairs should then represent different populations, whereas more closely situated pairs for the most part represent the same biological population. This simple explanation seems insufficient, however, to explain the apparent linear trend that emerges when geographic distance is replaced with downstream distance. Using this latter measure of distance has the effect of setting the East Greenland and Canadian samples further apart from the East Atlantic samples and, hence, of restoring a linear relationship with genetic differentiation. A biologically plausible explanation for the linear trend with downstream distance is that Greenland halibut larvae, during their long pelagic phase, are being transported with the ocean currents (Blindheim and Østerhus 2005). The resulting flow of larvae should, if at least some of them settle and survive along the route, represent a unidirectional gene flow along the path of the currents. Such gene flow is expected on theoretical grounds to eventually result in a linear relationship between genetic differentiation, measured as $F_{ST}/(1 - F_{ST})$, and distance along the current path (Rousset 1997). The observed linear relationship is therefore suggestive of ocean currents representing an important determinant of population structure in this species.

Independent support for the importance of larval drift in the Greenland halibut is the observation that while spawning takes place along the Norwegian coast, the spawning products (eggs and larvae) drift with ocean currents north and west of Svalbard, where they settle and feed (e.g., Godo and Haug 1989). All our samples from this spawning–nursery–feeding system (Halten Bank, Barents Sea Slope and Shelf, and Svalbard) were found to be genetically quite similar. These genetic results conform well to the findings of Godo and Haug (1989) and suggest that these samples may represent a single biological population. Hence, larval drift as a hypothesis for the observed genetic differentiation pattern has considerable support from direct observations on pelagic larvae in this species.

While a unidirectional flow of larvae and genes is a plausible explanation for the observed trend in genetic differentiation, several caveats apply. First, the results for East Greenland are especially important to our interpretation, and therefore further regional samples should be investigated in future to confirm this pattern. Second, a linear relationship is expected only after equilibrium has been attained between genetic drift within the constituent populations and gene

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flow among them, and it is unclear if conditions have remained stable for a long enough period to reach equilibrium. Third, even if the linear relationship between genetic differentiation and downstream distance is real and caused by gene flow, it could be generated by dispersal of adults rather than by passive drift of eggs and larvae.

Despite these precautions, the most parsimonous explanation for the observed spatial genetic patterns remains passive drift of pelagic eggs and larvae with ocean currents. This would imply an important role for ocean currents in shaping the genetic structure of Greenland halibut and may also apply for other species with pelagic early life history stages. For example, *Coryphaenoides rupestris*, *Macrourus berglax*, and *Antimora rostrata* all have similar life histories, and all are now severely depleted in the western North Atlantic (Devine et al. 2006). Further cues to the population structure of deepwater fish may be inferred indirectly from considerations of possible egg and larval transport routes and retention zones created by ocean currents and gyres. For example, retention systems around the Faroe Islands (Hansen 1992; Hansen et al. 1998) may largely retain spawning products in that area. While no major spawning ground is known in the vicinity of the Faroe Islands, spawning apparently occurs in this general area and the presence of retention zones could isolate this component from the rest of the East Atlantic. Overall, the present stock assessment for Greenland halibut conforms largely to our genetic findings; however, our results suggest that the Greenland and Faroe Islands stocks are presently incorrectly placed within the same management unit.

This study illustrates the potential importance of life history and oceanic current systems in the evolution of population structure in the North Atlantic and suggests that these considerations may apply to other species.

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Appendix A

Appendix appears on the following page.

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Table A1. Genetic variability at nine microsatellite loci, with allele richness (A), expected and observed gene diversity (H_E and H_O, respectively), and deviation from Hardy–Weinberg genotype proportions (F_{IS}).

Estimate	Hhl1	Hhl3	HhlC17	Hhl29	HhlA44	Hhl52	Hhl53	Hhl55	Hhl59
Barents Sea Shelf (BH)									
F_{IS}	0.224*	–0.022	0.026	0.016	0.032	–0.017	0.116	0.385**	–0.024
A	16.312	17.434	25.741	37.513	16.943	1.964	31.971	7.995	15.053
H_O	0.563	0.85	0.837	0.956	0.736	0.043	0.830	0.424	0.835
H_E	0.726	0.831	0.859	0.971	0.761	0.042	0.938	0.689	0.816
Null	0.1235						0.0584	0.2359	
Barents Sea Slope (BL)									
F_{IS}	0.287*	0.057	0.007	0.004	0.049	–0.011	0.229**	0.302**	–0.131
A	14.956	17.200	24.436	32.607	16.649	1.916	31.002	8.426	15.840
H_O	0.506	0.807	0.813	0.954	0.742	0.032	0.724	0.519	0.936
H_E	0.71	0.855	0.819	0.957	0.780	0.032	0.939	0.743	0.828
Null	0.1651						0.1263	0.1751	
Canada (CA)									
F_{IS}	0.282*	–0.019	0.009	–0.033	0.074	–0.034	0.178*	0.376**	0.026
A	14.354	16.245	28.365	35.061	13.194	2.000	35.000	7.867	15.267
H_O	0.441	0.817	0.853	1.000	0.656	0.082	0.789	0.475	0.767
H_E	0.613	0.802	0.861	0.968	0.708	0.079	0.960	0.760	0.787
Null	0.1597						0.0931	0.2273	
Faroe Island (FI)									
F_{IS}	0.222*	0.032	0.071*	0.008	–0.112	–0.021	0.191	0.374**	–0.021
A	14.640	16.368	27.243	36.942	14.029	1.980	36.443	8.979	13.563
H_O	0.573	0.811	0.809	0.959	0.813	0.052	0.767	0.472	0.819
H_E	0.736	0.837	0.87	0.966	0.731	0.051	0.948	0.753	0.803
Null	0.1218						0.1028	0.2271	
Greenland (GR)									
F_{IS}	0.364*	–0.028	0.084	–0.019	0.012	–0.005	0.195*	0.343**	0.022
A	15.793	14.355	27.879	32.243	16.070	1.771	36.406	9.134	19.174
H_O	0.462	0.830	0.768	0.970	0.790	0.020	0.776	0.489	0.800
H_E	0.725	0.807	0.838	0.952	0.800	0.020	0.963	0.745	0.818
Null	0.2196						0.1053	0.2043	
Halten Bank (HB)									
F_{IS}	0.284*	0.034	0.055	–0.005	0.029	–0.005	0.060	0.329**	–0.091
A	22.638	18.397	23.104	35.436	15.222	1.771	33.009	9.167	16.094
H_O	0.568	0.808	0.776	0.970	0.758	0.020	0.885	0.515	0.888
H_E	0.794	0.836	0.821	0.965	0.780	0.020	0.942	0.767	0.814
Null	0.1627						0.0284	0.1941	
Svalbard (SV)									
F_{IS}	0.363*	0.073	0.059	–0.003	–0.012	0.262	0.173	0.333**	–0.100
A	16.818	17.083	25.482	34.227	14.206	1.997	32.711	7.982	14.941
H_O	0.452	0.779	0.798	0.958	0.75	0.053	0.773	0.465	0.907
H_E	0.709	0.84	0.848	0.955	0.741	0.071	0.934	0.698	0.825
Null	0.2195						0.0917	0.1972	

Note: The null hypothesis (Null) of $F_{IS} = 0$ was tested with one-sided exact tests for each locus: *, $p < 0.05$; **, $p < 0.01$ (no correction for multiple tests). Null gives frequencies of null alleles estimated according to Chakraborty et al. (1992) using the MICRO-CHECKER software.

Appendix reference

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Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes

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Abstract: Herbivorous fishes show a clear latitudinal diversity gradient, making up a larger proportion of the fish species in a community in tropical waters than in temperate waters. One proposed mechanism that could drive this gradient is a physiological constraint due to temperature. One prediction based on this mechanism is that if herbivorous fishes could shift their diet to animal material, they would be better able to grow, survive, and reproduce in cold waters. We tested this prediction on the omnivore *Girella nigricans* under different temperature and diet regimes using RNA–DNA ratios as an indicator of performance. Fish had increased performance (100%) at low temperatures (12 °C) when their diet was supplemented with animal material. In contrast, at higher temperatures (17, 22, and 27 °C) fish showed no differences between diets. This indicates that omnivorous fishes could increase their performance at low temperatures by consuming more animal matter. This study supports the hypothesis that a relative increase in the nutritional value of plant material at warmer temperatures could drive the latitudinal diversity gradient in herbivorous fishes.

Résumé : Les poissons herbivores se répartissent selon un gradient latitudinal de diversité, dans lequel ils représentent une proportion plus grande des poissons de la communauté dans eaux tropicales que dans les eaux tempérées. Un des mécanismes proposés pour expliquer ce gradient est une contrainte physiologique reliée à la température. Une des prédictions découlant de ce mécanisme est que, si les poissons herbivores pouvaient changer leur régime alimentaire pour augmenter le matériel animal, ils seraient mieux capables de croître, de survivre et de se reproduire dans les eaux froides. En utilisant les rapports ARN–ADN comme indicateurs de performance, nous avons testé cette prédiction chez l'omnivore *Girella nigricans* à différentes températures et sous divers régimes alimentaires. Les poissons ont une performance accrue (100 %) à basse température (12 °C) lorsque leur régime est additionné de matière animale. En revanche, aux températures plus élevées (17, 22 et 27 °C), il n'y a pas de différence chez les poissons, quel que soit le régime alimentaire. Cela indique que les poissons omnivores pourraient améliorer leur performance à basses températures en consommant plus de matière animale. Notre étude appuie l'hypothèse qui veut qu'une augmentation relative de la valeur nutritive de la matière végétale aux températures plus élevées pourrait expliquer le gradient latitudinal de diversité chez les poissons herbivores.

[Traduit par la Rédaction]

Introduction

Is poor-quality food better when warm? Is high-quality food better when cold? If so, the ideal diet for an ectotherm could vary with body temperature, potentially explaining broad geographic patterns in species' distributions. Herbivorous ectothermic vertebrates such as fishes and reptiles show striking latitudinal gradients in diversity and abundance that are potentially related to temperature's effect on physiology (Horn 1989; Zimmerman and Tracy 1989). Although multiple mechanisms could act simultaneously to drive these patterns, Floeter et al. (2005) conclude that the most probable mechanism is that herbivorous fishes cannot meet their energetic demands in temperate waters (Gaines and Lubchenco 1982; Horn 1989; Horn and Ojeda 1999). This mechanism, which is based on the interaction of temperature and food quality on fish physiology, may simultaneously explain both the latitudinal diversity gradient in herbivorous fishes and limited evolution of herbivorous fishes in temperate waters. Temperature affects many physiological systems and processes (Jobling 1994); therefore, to determine if a digestive constraint due to temperature limits the geographical distribution of herbivorous fishes requires simultaneously controlling diet across temperature and measuring physiological differences.

Temperature, food quality, and body size are thought to be the most important determinants of food assimilation

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(Kooijman 2000). Tropical fish species have evolved the ability to survive on a low-quality herbivorous diet, whereas temperate and polar species generally have not, despite higher standing stocks of plant material at higher latitudes (Harmelin-Vivien 2002; Floeter et al. 2004). Numerous studies have attempted to determine the simultaneous effects of temperature and diet quality and quantity on growth or condition in fishes (for recent examples, see Mischke et al. 2001; Deng et al. 2002; Johnson et al. 2002). Almost none of this work has focused specifically on herbivorous species. Studies similar to these, if conducted on herbivorous fishes, may help understand how temperature and diet may interact to influence the geographic distributions of trophic groups such as herbivores.

Plant material is a low-quality food and difficult to assimilate (Horn 1989). The dual challenge of low-quality diet and low assimilation efficiency means that herbivorous fish must feed more often than carnivorous species to meet their energetic demands (Arrington et al. 2002). This is likely possible in temperate shallow-water habitats where plant material is generally more available than animal prey (Gaines and Lubchenco 1982). However, at low temperatures, feeding rate declines (Jobling 1994), and because herbivorous fish require nearly constant food intake to survive (Arrington et al. 2002), they may experience disproportionate metabolic costs at low temperatures compared with carnivores if feeding rates experience greater declines than metabolic rates.

Omnivorous fishes present a unique opportunity to test the hypothesis that temperature limits herbivory. Extension of the hypothesis to omnivory predicts that the relative importance of plant material to an omnivore's diet will decline in cold water. Additionally, increasing diet quality by adding animal matter to the diet of omnivores can have nonadditive effects, where growth rate may increase more than expected by the addition of the animal matter alone due to positive effects on the digestion of algae consumed with the animal matter (Bjørndal 1991).

Growth is commonly used to assess an organism's reaction to environmental conditions; however, estimation of this parameter is difficult over short time intervals characteristic of lab studies (Buckley et al. 1999). We chose RNA–DNA ratios to indicate a short-term change in performance in response to temperature and diet (Buckley et al. 1999; Buckley and Szmant 2004). The RNA–DNA ratio reflects the protein synthesis capacity of a tissue and indicates the nutritional and energetic condition of the organism (Buckley 1984; Stillman et al. 1994; Dahlhoff and Menge 1996). We used RNA–DNA ratios as an index of performance. RNA–DNA ratios have been used in this manner in a wide range of organisms (Bulow 1987; Dahlhoff and Menge 1996; Buckley and Szmant 2004).

Determining if a digestive constraint due to temperature limits the geographical distribution of herbivorous fishes requires controlling for digestive differences across temperature, as temperature also affects many other physiological systems and processes. Therefore, it is necessary to determine if the organism could survive and experience increased performance at colder than normal temperatures if the organism were fed a higher-quality diet. To better understand if temperature's effect on digestion limits the poleward thermal limit of herbivorous fishes, we controlled both diet and temperature in the lab to determine if an increase in diet quality increased an omnivorous fish's performance at cold temperatures. We chose the opaleye, *Girella nigricans* (Ayres), a common member of the rocky reef fish assemblage in Baja California and southern California (Love 1996). This species shows dramatic changes in its ecology at low temperatures. At the northern end of its range, *G. nigricans* declines in abundance at low temperatures (Floeter et al. 2005). Additionally, the feeding behavior of this species changes across its range, with animal material becoming more important as temperature declines (Behrens 2005). Because *G. nigricans* experiences a wide range of temperatures across its range (Norris 1963) and readily accepts a wide range of food items in the lab, it is an ideal organism on which to test the simultaneous effects of diet and temperature on performance. We predicted that fishes fed plant material would show a stronger increase in performance with an increase in temperature than fish fed animal material. Here we find that temperature alters the relative performance of *G. nigricans*, where performance increases with diet quality at low temperatures, but the relationship reverses at high temperatures.

Materials and methods

Sampling and acclimation

We collected opaleye from shallow subtidal habitats in the Santa Barbara harbor (34°24.241′ N, 119°41.519′ W) in southern California. This study population was from the northern region of the species geographic range, where individuals commonly feed primarily on benthic algae (Behrens 2005). Twenty-four juvenile to subadult *G. nigricans* (7.9–15.7 cm standard length (SL)) were captured with hook and line, immediately deposited in separate plastic bags containing fresh seawater, and transported to the laboratory. Fish were housed in one of 24 compartments in 12–38 L aquaria divided by partitions for up to 5 days at ambient temperatures (15 °C) and fed algae (*Ulva* spp.) ad libitum. Once fish began feeding and defecating, we initiated temperature changes in each of four temperature treatment blocks (three aquaria each) of aquaria at a rate of 2 °C·day^{-1} until experimental temperatures were reached. We staggered the initiation of the change of temperature so that all fish would reach the experimental temperature on the same date.

Diet–temperature experiment

Once all temperature blocks reached the appropriate experimental temperatures (12, 17, 22, 27 °C), which encompassed nearly the entire temperature range experienced by *G. nigricans* (11–27 °C; Norris 1963), we measured the standard length and weight of all fish and returned them to the appropriate aquarium compartment. The fish on one side of the aquarium partition were fed algae (*Ulva* spp.) ad libitum, and the fish on the other side were fed algae (*Ulva* spp.) ad libitum plus squid at a rate of 1% of the specimen's body mass per day. We designated these two feeding treatments the herbivory and omnivory treatments, respectively. We monitored daily consumption rates of both fish fed algae and fish fed algae plus squid by determining the difference between the wet masses fed one day and the food still remaining in the next day. After 28 days, we euthanized all specimens with MS-222 (5 g·L^{-1} tricaine methanesulfonate)

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and collected white muscle samples. We immediately froze all white muscle samples at –70 °C. To increase sample sizes, we conducted two sequential trials using identical methods.

Sample analysis

To determine RNA–DNA ratios of the white muscle samples, we determined RNA and DNA concentrations in each sample using ethidium bromide fluorescence, following the method of Bentle et al. (1981), as modified by Dahlhoff and Menge (1996). We thawed white muscle samples on ice and weighed and homogenized these samples in 10 volumes of 2 mol·L^{-1} NaCL with a hand-driven glass homogenizer. We incubated 50 µL from each sample in a 1.5 mL solution containing 0.005 mg ethidium bromide and 0.15 mg proteinase K at 37 °C for 60 min. After this initial incubation, we added 1.0 mL buffer (80 mM Tris–HCl, pH 7.5 at 20 °C) and then measured fluorescence at 365 nm excitation and 590 nm emission using a Turner Biosystems TD-100 luminescence spectrofluorometer. We determined fluorescence due to RNA and DNA by sequential digestion of each nucleic acid using 50 µL RNAse I (1.0 mg·mL^{-1}, bovine thymus) followed by a 30-min incubation and DNAse I (0.5 mg·mL^{-1}, bovine pancreas) followed by a 30-min incubation. Then, we estimated RNA and DNA concentrations from a standard curve calculated by measuring the fluorescence of known quantities of RNA and DNA (Sigma calf thymus, 0–4 µg; Sigma calf liver RNA, type IV, 0–8 µg).

Statistical analysis

We performed a split-plot analysis using a generalized linear model (GLM) to determine the effects of diet and temperature on RNA–DNA ratios, including the effects of fish length and trial. We included only the significant interaction terms in the final split-plot model. During the second trial, fishes on the omnivorous diet at the coldest temperature (12 °C) rarely consumed squid, which effectively removed the diet treatment at this temperature. Therefore, we excluded the 12 °C treatment from the second experimental run from the split-plot analysis, but used the data in all other analyses that used percent algal material in the diet as the independent variable. To investigate how diet treatments changed among the temperature treatments (due to feeding differences), we regressed the percent animal material in the diet against temperature. Additionally, we regressed the residual daily consumption of algal material and animal material, after the effect of fish length was removed, against temperature. To determine how RNA–DNA ratios changed as the amount of animal material in the diet increased, we used a GLM to determine the effect of temperature and the amount of animal material in the diet on RNA–DNA ratios, after the effect of fish length was removed. Excluding data from the second trial of the split-plot analysis did not introduce bias into the analysis and did not impact our ability to use the full set of data to test the hypothesis with a second GLM method. After confirming that the data met the assumptions of the statistical models (normality and homogeneity of variances), we performed all analyses on nontransformed data using JMP (SAS Institute Inc. 2002).

Results

Diet and temperature influenced the RNA–DNA ratios of the omnivorous study species (Fig. 1). The effect of diet was dependent on the experimental temperature (Table 1, split-plot analysis of variance (ANOVA), diet × temperature interaction, $F_{[3,16]} = 4.001$, $p = 0.027$). At 12 °C, fish fed an omnivorous diet had higher (100% increase) RNA–DNA ratios than fish fed an herbivorous diet ($F_{[1,16]} = 6.457$, $p = 0.022$; Fig. 1), whereas at higher temperatures (17, 22, and 27 °C), the diet did not affect the RNA–DNA ratio (17 °C, 19% increase, $F_{[1,16]} = 1.637$, $p = 0.219$; 22 °C, 18% decrease, $F_{[1,16]} = 0.816$, $p = 0.380$; 27 °C, 34% decrease, $F_{[1,16]} = 3.072$, $p = 0.100$). At these higher temperatures, there was relatively low power to detect differences between diet treatments (17 °C, power = 0.225; 22 °C, power = 0.136; 27 °C, power = 0.378). A moderate increase in sample size (33%) at 27 °C may have allowed us to detect a significant difference between diet treatments. However, extremely large increases in sample size would have been required to detect the observed differences between the diet treatments at 17 °C (240%) and 22 °C (476%). Therefore, it seems unlikely that low statistical power led to the finding of no difference between diets at the intermediate temperatures (17 °C and 27 °C). Additionally, there were changes in performance with temperature within diet treatments. Fish fed an omnivorous diet showed a significant decline in RNA–DNA ratios at higher temperatures ($F_{[3,16]} = 3.437$, $p = 0.039$; Fig. 1). In contrast, fish fed an herbivorous diet showed a moderate, but nonsignificant, increase in RNA–DNA ratios from 12 °C to the higher temperatures ($F_{[1,15]} = 4.170$, $p = 0.059$; Fig. 1).

Although fish fed the omnivorous diet received 1% body mass of animal material per day, diet treatments varied among temperature treatments because differences in consumption of both algae and squid among temperatures (Fig. 2). The percent animal material in the diet declined as the experimental temperature increased ($R^2 = 0.506$, $F_{[1,22]} = 22.519$, $p < 0.001$; Fig. 2*a*). After we removed size-related differences in feeding rate, the amount of algae consumed ($R^2 = 0.637$, $F_{[1,21]} = 18.442$, $p < 0.001$; Fig. 2*b*) and animal material consumed ($R^2 = 0.173$, $F_{[1,22]} = 4.604$, $p = 0.043$; Fig. 2*c*) increased with temperature. The decline in the percent animal material was driven by relative differences in the change in the amount of algal and animal material consumed at the various temperatures (Fig. 2).

Because of feeding differences among individuals within a temperature treatment, we could determine how changes in the percent animal material at a given temperature affected the RNA–DNA ratio. After removing the effects of fish size and time, the effect of the percent animal material in the diet on RNA–DNA ratios changed across temperature treatments (temperature × percent animal material, $F_{[3,40]} = 3.421$, $p = 0.026$; Fig. 3). The slope of the relationship between RNA–DNA ratio and the percent animal material in the diet increased (172%) with declining temperature from the highest temperature (27 °C) to the lowest temperature (12 °C) (Fig. 3).

Discussion

Diet and temperature interacted to determine performance in *G. nigricans*. At low temperatures, *G. nigricans* performed better when fed an omnivorous diet than an herbivorous diet. In contrast, performance under the two diets was

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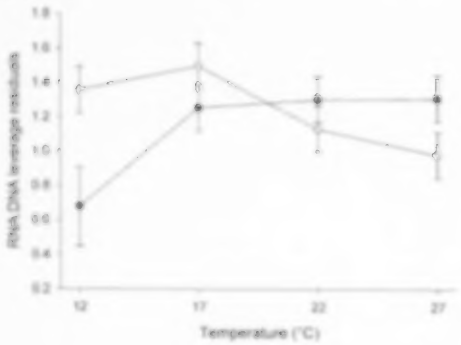
Fig. 1. Mean residual RNA–DNA ratios for the two diet treatments (herbivore, algae ad libitum; omnivore, algae ad libitum plus 1% body mass in squid per day) plotted against temperature. The effect of temperature on RNA–DNA ratio was dependent on diet (diet × temperature interaction, $F_{[3,16]} = 4.001$, $p = 0.027$). Solid circles represent the herbivore treatment; open circles represent the omnivore treatment. Error bars represent ±1 standard error.



not significantly different at higher temperatures. This was at least partially because fish on the omnivorous diet consumed a higher proportion of algae as temperature increased. The pattern became clearer when the actual amount of animal material in the diet was considered. At low temperatures, the relationship between performance and the amount of animal material in the diet was positive. However, at high temperatures, the slope of the relationship reversed, with performance declining with an increase in the amount of animal material in the diet. The low performance of the herbivorous diet in cold temperatures supports the hypothesis that a thermal constraint on digestive physiology limits the distribution of herbivorous fishes to warm waters. The decline in performance at high temperatures suggests a cost to carnivory at high temperatures, which may be related to the extensive evolution of herbivorous fishes in tropical waters. However, it should be noted that this experiment was conducted on a cold-water population and the potential for local adaptation should be considered when extrapolating these results to warm-water populations.

RNA–DNA ratios are commonly used indicators of potential for protein synthesis, growth, and nutritional condition in a wide range of organisms (Frantzis et al. 1992; Dahlhoff and Menge 1996; Caldarone et al. 2003). RNA–DNA ratios vary in response to many environmental and biological conditions, but typically minimum values are greater than 1.0. When the ratio falls below 1.0, it is usually attributed to physiological stress, such as food limitation (Kono et al. 2003) or hypoxia (Aday et al. 2000). The RNA–DNA ratios in this study suggest that *G. nigricans* experienced physiological stress at the lowest and highest experimental temperatures, but the stress was dependent on diet. At 12 °C, the mean ratio for fish fed exclusively algae was 0.68 (standard error (SE) = 0.23). In contrast, those fish at the same temperature with a diet that was supplemented with animal material had a mean ratio of 1.36 (SE = 0.13). Although not statistically different, at the highest temperature (25 °C), fish on the omnivorous diet had a mean ratio of 0.98 (SE = 0.14), whereas those fish on the herbivorous diet had a mean ratio of 1.31 (SE = 0.13). The difference between the two diet treatments indicated that the stress was driven by diet rather than by the thermal tolerances of *G. nigricans*.

Because increased diet quality should be beneficial in nearly all cases, the finding of a negative effect of animal material in the diet at high temperatures on performance was unexpected, especially as carnivorous fishes are common at all latitudes and temperatures. Low temperatures and animal material in the diet can independently suppress gut passage rate (Fänge and Grove 1979; Klumpp and Nichols 1983; Fris and Horn 1993). Diet-related suppression of gut passage rate at high temperatures in herbivores might limit food consumption below minimum levels required to meet their increased metabolic demands at high temperatures. However, further research into the effects of temperature and food quality on digestive physiology is needed to elucidate the cause of this result.

The optimal temperature for digesting plant material may differ from the optimal temperature for metabolism. Because of their low-quality diet, herbivorous fishes may need to reduce energy loss by selecting low temperatures but may also require high temperatures for efficient digestion and growth. Herbivorous lizards show such a conflict because of their thermal physiology and are able to actively thermoregulate by basking to meet their present physiological needs (Wikelski and Trillmich 1994). Pulgar et al. (2003) found that the southern hemisphere omnivore *Girella laevifrons* selects intermediate temperatures (16–19 °C) on a high-quality diet (bivalves), but selects lower temperatures (10–13 °C) when fed a lower-quality diet (algae). These authors concluded that *G. laevifrons* selects low temperatures to conserve energy when fed a low-quality diet and selects intermediate temperatures when fed a high-quality diet to optimize digestion. In contrast, our findings suggest that fish perform better at high temperatures when fed a low-quality diet. Because most subtidal marine fishes live in a relatively homogeneous thermal environment, few will be able to choose the temperature that best balances the needs for energy conservation (low temperatures) and digestion (high temperatures).

Feeding behavior of fishes can be affected by many factors, including temperature, and is thought to be driven by the nutrient requirements of the fish (Clements and Raubenheimer 2006). Both the pinfish, *Lagodon rhomboides*, and spottail pinfish, *Diplodus holbrooki*, consume a greater proportion of animal material as water temperature declines, and refused to consume algae below 17 °C (Mark Hay, Georgia Institute of Technology, School of Biology, Atlanta, GA 30332, unpublished data). Feeding behavior in *G. nigricans* changes across its range. In the wild, fish eat significantly more animal material in cold than in warm locations (Behrens 2005). This parallels our results from the laboratory for *G. nigricans*. Although the mass of animal material in the diet was fixed in our experiment, the proportion of animal material included by the fish in their diet was highest in the cold-water treatment. The higher RNA–DNA ratio for the omnivorous treatments versus the herbivorous treatments in cold water suggests that this behavioral change is adaptive. RNA–DNA ratios are likely related to fitness as they are related to potential protein synthesis. Protein syn-

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Table 1. Split-plot GLM on the effects of temperature, diet, aquarium, trial, time, and fish length on the RNA–DNA ratio of *Girella nigricans*.

Source of variation	df	MS	*F* ratio	*p* value
Temperature	3	0.1954	2.1893	0.1091
Diet	1	0.1032	0.9748	0.3381
Aquarium (within temperature)	19	0.0841	0.7950	0.6865
Trial	1	0.0418	0.3946	0.5388
Fish length	1	0.0799	0.7554	0.3975
Diet × temperature	3	0.4236	4.0013	0.0265
Error	16	0.1058		

Note: Temperature: 12, 17, 22, 27 °C; diet: herbivore, omnivore. We treated aquarium nested within temperature as a random variable.

Fig. 2. Change in components of the omnivore feeding treatment at the experimental temperatures: (*a*) regression of percent animal material in the diet against temperature ($R^2 = 0.506$, $F_{[1,22]} = 22.519$, $p < 0.001$); (*b*) regression of residual wet mass of algal material in the diet against temperature, after the removal of the effect of fish size ($R^2 = 0.637$, $F_{[1,21]} = 18.442$, $p < 0.001$); (*c*) regression of percent animal material in the diet against temperature, after the removal of the effect of fish size ($R^2 = 0.173$, $F_{[1,22]} = 4.604$, $p = 0.043$).

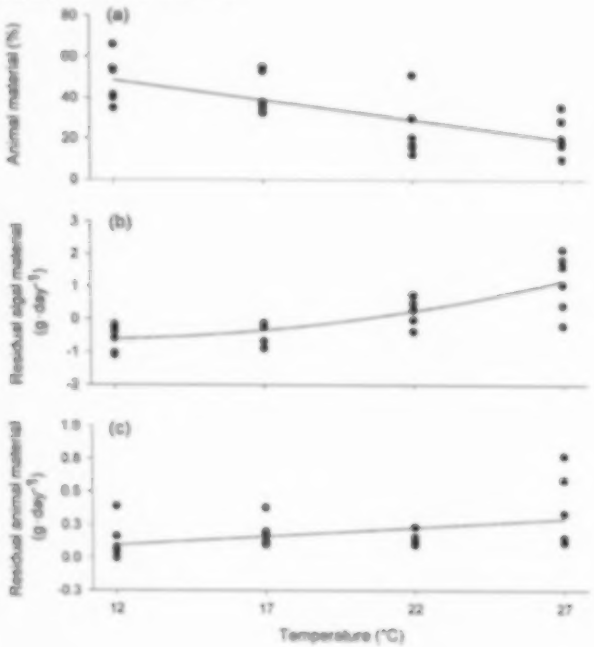
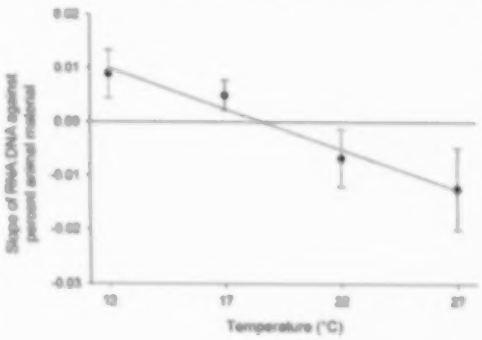


Fig. 3. Slope of individual regression lines of residual RNA–DNA ratios plotted against percent animal material for each of the four temperature treatments (temperature × percent animal material, $F_{[3,40]} = 3.421$, $p = 0.026$). Residual RNA–DNA ratios were used to remove the effect of fish size before initial regression against temperature. Error bars represent ±1 standard error.



thesis is the single most energetically expensive physiological process in fishes (Carter and Houlihan 2001); thus increased RNA–DNA ratios likely indicate increased energy reserves for other processes, e.g., reproduction.

If RNA–DNA ratios can be extrapolated to the fitness of the organism, then our results may show the basis for a selective advantage for herbivorous fishes in the tropics but not in temperate and polar waters. Figure 2 illustrates the potential for temperature-dependent selection, where herbivory should be selected against at low temperatures, whereas carnivory may be selected against at high temperatures (especially if animal material is more difficult to obtain than algal material). This selection against herbivory in temperate and polar waters might explain the relatively low rates of evolution of herbivorous fishes in cold waters and the resulting latitudinal diversity gradient in herbivorous fishes (Gaines and Lubchenco 1982; Horn 1989; Floeter et al. 2005). This seems more parsimonious than the scenario of limited time for evolution and range expansion of herbivorous fishes in cold waters (Mead 1970). The selection against carnivory at high temperatures may further explain the extensive evolution of strictly herbivorous fishes in the tropics and why omnivory would not be favored at all temperatures. This further reduces the reliance on secondary explanations, such as competition, to explain strictly herbivorous fishes in the tropics as competition for food is likely intense in both temperate and tropical systems.

Although the results of the present study show important findings that further our understanding of the potential mechanisms underlying the geographic distribution of herbivory in fishes, they should be extrapolated to all herbivorous fishes with caution. This study was performed on a single species and lacks generality. To better understand if these findings can be generalized to most herbivorous fishes, this type of experiment should be repeated with a range of species from temperate and tropical habitats and with various evolutionary histories.

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In conclusion, the effect of temperature on performance of *G. nigricans* is dependent on diet. Fish fed an omnivorous diet had greater performance at low temperatures than those fed an herbivorous diet. In contrast, fish fed an herbivorous diet had greater performance at high temperatures than fish fed an omnivorous diet. These results lend support to the existence of a physiological constraint owing to temperature limiting the evolution of herbivory in cold waters and therefore driving the latitudinal diversity gradient in herbivorous fishes.

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Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish

Thomas Mehner, Peter Kasprzak, and Franz Hölker

Abstract: Evolutionary hypotheses for diel vertical migrations (DVM) of aquatic animals include foraging opportunity, predator avoidance, and bioenergetics efficiency. Here we test which hypothesis predicts DVM in the small planktivorous coregonids vendace, *Coregonus albula*, and Fontane cisco, *Coregonus fontanae*, in a deep oligotrophic lake. Densities and population depths of young-of-the-year and larger coregonids were determined by hydroacoustics during day and night over 10 consecutive months. Depth distributions of predator-like fishes and zooplankton resources were recorded as well. Furthermore, Secchi depth, water temperature, oxygen concentrations, and pH values were determined at each sampling month. A DVM of the coregonids was observed in all months. Population depths during the night were significantly correlated to water temperatures, oxygen concentrations, and pH values. In contrast, the vertical distributions of predators or resources were not correlated with the coregonid depth distribution. These results do not correspond to the feeding opportunity or predator avoidance hypotheses of DVM, but support in part the bioenergetics efficiency hypothesis. However, the stable migration pattern of fishes over all months despite substantial changes in biotic and abiotic conditions suggests that diel migrations in the coregonids are a genetically fixed behavioral trait to minimize the anticipated potential predation risk in the illuminated water layers during daytime.

Résumé : Parmi les hypothèses évolutives évoquées pour expliquer les migrations verticales journalières (« DVM ») des animaux aquatiques, il y a celles des possibilités alimentaires, de l'évitement des prédateurs et de l'efficacité bioénergétique. Nous vérifions laquelle de ces hypothèses permet d'expliquer la DVM des petits corégonidés planctonophages, le corégone blanc, *Coregonus albula*, et le corégone de Fontane, *Coregonus fontanae*, dans un lac oligotrophe profond. Nous avons déterminé par hydroacoustique les densités et les répartitions en profondeur des populations de jeunes de l'année et d'adultes des corégonidés durant le jour et la nuit pendant 10 mois consécutifs. Nous avons aussi précisé les répartitions en profondeur des poissons de type prédateur et des ressources en zooplancton. Nous avons, de plus, mesuré la profondeur de Secchi, la température de l'eau, les concentrations d'oxygène et les valeurs de pH à chaque mois de l'échantillonnage. Les corégonides font des DVM à tous les mois de nos observations. Durant la nuit, les profondeurs choisies par la population sont en corrélation significative avec les températures de l'eau, les concentrations d'oxygène et les valeurs de pH. En revanche, les répartitions verticales des prédateurs et des ressources ne sont pas en corrélation avec la répartition en profondeur des corégonidés. Ces résultats n'appuient pas les hypothèses des possibilités alimentaires, ni de l'évitement des prédateurs de la DVM, mais elles soutiennent en partie celle de l'efficacité énergétique. Cependant, la stabilité des patrons de migration des poissons au cours de l'ensemble des mois d'échantillonnage, malgré les changements importants dans les conditions biotiques et abiotiques, laisse croire que les migrations journalières chez les corégonidés sont des caractéristiques comportementales fixées génétiquement visant à minimiser le risque potentiel de prédation dans les couches d'eau éclairées pendant la journée.

[Traduit par la Rédaction]

Introduction

Diel vertical migrations (DVM) were reported from a wide range of aquatic animals. The regular DVM pattern is a stay in deep, dark water layers during daytime followed by an ascent and stay in higher water layers during dusk and at night, with the descent back to the deep layers occurring during dawn. DVM are well studied in zooplankton populations, including *Daphnia*, *Chaoborus*, copepods, and euphausiids (reviewed by Lampert 1993; Hays 2003), and freshwater and marine fish (Rudstam and Magnuson 1985; Huse and Korneliussen 2000; Scheuerell and Schindler 2003). Mechanistic explanations differentiate between proximate and ultimate factors (Pijanowska 1993). There is a broad consensus that in both fish and zooplankton, the rela-

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tive change in illumination strength at dusk and dawn is the proximate factor triggering the onset of the upward and downward migrations, respectively (Hamrin 1986; Ringelberg 1991; Lampert 1993). The ultimate (evolutionary) causes for DVM can be summarized into three hypotheses, namely feeding opportunity, predator avoidance, and bioenergetics efficiency hypotheses (Hays 2003; Scheuerell and Schindler 2003).

The feeding opportunity hypothesis claims that animals follow their prey in space and time to maximize foraging and subsequent growth rates, although empirical evidence in fish is rare (Levy 1990). More often, the avoidance of visual predators by the prey was found to explain the preference of dark habitats during daytime (Clark and Levy 1988; Lampert 1993; Hays 2003). The third hypothesis of bioenergetics efficiency assumes that there is an energetic advantage if animals can feed in the warm, food-rich water layers at night, but digest in the colder, deeper layers during daytime, thus maximizing their growth rate (Bevelhimer and Adams 1993).

A further differentiation can be made with respect to the evocation of migrations. Empirical research has provided evidence that concentrations of kairomones released by planktivorous fish are used by *Daphnia* to evaluate their predation risk (Ringelberg 1991). Consequently, migration is inducible by an increase in predator densities, and an inducible trait reflects the variable phenotypic expression of a single genotype (Pijanowska 1993). In contrast, the coexistence of migrating and nonmigrating *Daphnia* clones was reported as the source of observed variability in DVM patterns (Weider 1984; De Meester et al. 1995). Accordingly, DVM can be considered as a genetically fixed strategy reflecting genetic polymorphism in zooplankton populations. Although this dichotomy between fixed and induced behavioral traits has received some attention in discussing DVM patterns in zooplankton (Pijanowska 1993), no study has formally analyzed whether fish DVM is inducible or genetically fixed. However, a genetical fixation of DVM was not reported in any of the available studies (e.g., Hamrin and Persson 1986; Bevelhimer and Adams 1993; Scheuerell and Schindler 2003).

Here we study DVM patterns of two small coregonid fishes, the European vendace (*Coregonus albula*) and the Fontane cisco (*Coregonus fontanae*), in Lake Stechlin (Germany). These coregonids are primarily zooplanktivorous fishes inhabiting the pelagic area of deep oligo- and mesotrophic lakes (Hamrin 1986; Garcia et al. 2006). A DVM in vendace was reported from a range of lakes (Northcote and Rundberg 1970; Hamrin 1986; Sydänoja et al. 1995). However, no attempt has been made to explore the evolutionarily adaptive value of these regular habitat shifts. Furthermore, it is not known whether the migration patterns in coregonids are genetically fixed or inducible. We used hydroacoustic sampling during day and night over 10 months to cover a wide range of abiotic conditions and resource and predator densities. We explored whether the adaptive value of the DVM in the coregonids can be explained by the feeding opportunity, the predator avoidance, or the bioenergetics efficiency hypotheses. We expected that population depths or migration amplitudes would be modified or even induced or interrupted by the seasonal changes in abiotic and biotic environments, in line with the assumption that the DVM is a variable phenotypic expression of a single genotype.

Materials and methods

The study was conducted in the deep, oligotrophic Lake Stechlin (53°10′N, 13°02′E; 4.3 km² surface area), situated approximately 120 km north of Berlin in the Baltic lake district of Germany (Fig. 1). Mean and maximum depths are 22.8 m and 69 m, respectively. A total of 13 fish species has been reported in Lake Stechlin, among which the European vendace and the smaller endemic Fontane cisco dominate the pelagic fish community with about 70% and 30% of total numbers, respectively (Helland et al. 2007). Other fish species that occasionally occur mainly above the thermocline are roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*), and Eurasian perch (*Perca fluviatilis*) (Anwand et al. 2003).

Diel differences in vertical fish distribution were estimated from hydroacoustic recordings. Echosoundings were conducted monthly between March and December 2005 at dates not more than 1 week distant from the full moon (29 March, 18 April, 23 May, 13 June, 18 July, 9 August, 21 September, 17 October, 14 November, 13 December 2005). Ice cover prevented samplings in January and February. A SIMRAD EY-60 split-beam echosounder with 120 kHz operating frequency (7° × 7° circular transducer, type ES 120-7C) was applied. The equipment was calibrated twice that year (February on ice and in September) with a standard copper sphere of 23.0 mm diameter (reference target strength (TS) = –40.4 dB at 1490 m·s^{-1} sound speed). However, the measured TS did not deviate by more than 0.1 dB from the reference value. Furthermore, there were no changes in angle sensitivity and little changes in angle offset (shift of –0.04 athwart) or 3 dB beam widths (maximum shift 0.19°, i.e., <3% variability) according to the calibrations. Additional on-axis calibrations were conducted in May and November, and again TS did not deviate by more than 0.1 dB from the reference value. Pulse duration during all surveys was 256 µs, resulting in a sample interval of 0.047 m at a receiver bandwidth of 8.71 kHz. Pulse interval was set to 0.3 s at an approximate boat speed of 6 km·h^{-1}. The sound speed was adjusted to average water temperature according to the equation implemented in the SIMRAD software (SIMRAD, Kongsberg, Norway). All surveys consisted of five nonoverlapping cross transects in the central and northern basins of Lake Stechlin (45–65 m deep, 900–1200 m long) with a total length of 5.5 km (about 8000 pings; Fig. 1). To keep all surveys comparable in spatial cover, more transects could not be included because the short nighttime period of full darkness during summer defined the maximum duration of each survey.

Data analysis was performed by the Sonar 5Pro software, version 5.9.5 (Balk and Lindem 2005). Upper echo thresholds for file conversion were set to –80 dB (volumetric backscattering strength, S_v) and –75 dB (TS). Single-echo detection (SED) was based on 0.8 to 1.2 relative pulse widths, a one-way beam compensation of 3 dB, and a maximum phase deviation of 0.8. The recorded file of each transect was split into 13 separate 5 m thick depth layers, starting outside of the near-field range of the transducer at 1 m water depth (1–6, 6–11, ..., 61–66 m). These layers

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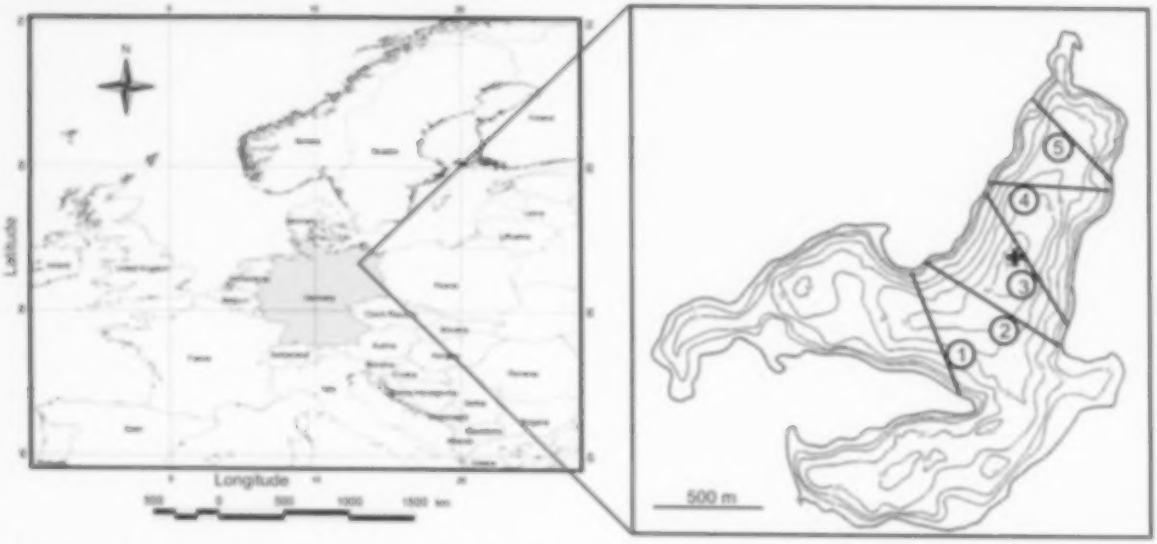
Fig. 1. Map of Europe with Germany and location of Lake Stechlin highlighted, and contour map with water depth isolines (10 m range) of Lake Stechlin. The five transects sampled with the echosounder are indicated by lines and numbers; the plus sign (+) represents the location for abiotic and zooplankton sampling.



were separately analyzed to prevent biased estimates of total fish densities due to lack of homogeneity in vertical distribution. Later inspection of the files indicated that the first layer frequently contained numerous echoes from gas bubbles induced by strong winds during the surveys. Accordingly, this layer was excluded, and all results of fish densities and vertical distributions are based on the depth range between 6 and 66 m. The average Sawada index (N_v; number of fish per effective reverberation volume) per survey ranged between 0.0008 and 0.016 and thus was below the recommended critical threshold of 0.04 (Sawada et al. 1993), except for the March surveys where it was 0.051 and 0.054 during the daytime and nighttime surveys, respectively. This indicates that the measured TS values were likely not biased by overlapping multiple SEDs.

S_v per depth layer was converted into volumetric densities (D_{vol}; individuals·1000 m^{-3}) according to the TS frequency distribution of single echoes in 1 dB classes between –60 dB and –30 dB by

$$D_{vol} = \frac{S_v}{\frac{1}{N}\sum_{k=1}^{K} n_k \mathrm{TS}_k} = \frac{10^{S_v/10}}{\frac{1}{N}\sum_{k=1}^{K} n_k 10^{\mathrm{TS}_k/10}}$$

where S_v and TS are mean volume backscattering strength and target strength (in dB), respectively; N is the total number of fish; K is the number of size classes (here 30); k indicates the kth size class; and n_k the number of fish in size class k (Bodholt (1990), cited in Balk and Lindem (2005)).

During the daytime surveys, however, the number of SEDs per depth layer was <10 in the upper six depth layers down to 36 m. In this case, layer-specific density estimates would have been based on uncertain fish length distributions. To avoid this bias, all SEDs in the 6–36 m depth layers of the five transects per survey were summed, and the conversion of S_v into fish densities for the 6–36 m depth layers during daytime was based on these cumulative TS frequency distributions. Total densities per layer were split into values reflecting either small or large coregonids, based on the TS–length regression for vendace

$$\mathrm{TS\ (dB)} = 25.5\log_{10}(\text{total length (cm)}) - 70.9$$

(Mehner 2006). Because the two coregonid species could not be discriminated by the hydroacoustics, the fish size groups were chosen to reflect roughly either young-of-the-year (2.5–8 cm total length, equivalent to a TS of –60 to –48 dB) or juvenile and adult (8–24 cm total length, –48 to –36 dB) vendace and Fontane cisco. The maximum size of the coregonids in Lake Stechlin is about 25 cm, and no other species of that size occur in the pelagic area below the thermocline (Mehner and Schulz 2002; Anwand et al. 2003). Targets with TS in the range of –36 to –30 dB were considered to be potential predators of the coregonids with 25–50 cm total length. According to earlier observations, the only predator in this size range occurring in the upper pelagic layers of Lake Stechlin is perch (Anwand et al. 2003).

The volumetric densities per fish size group were averaged over the 12 water layers to obtain group-specific densities per transect. The average volumetric density per survey was calculated from the five transects, weighted by the ping number per transect. The population depth (PD; in metres) of the fish groups per transect during day or night at each sampling date was calculated as weighted average by

$$\mathrm{PD} = \frac{\sum_{i=1}^{a} \frac{D_i}{\overline{D}} z_i}{a}$$

with D_i is the density of group in depth layer i, $\overline{D}$ is the average group density over all depth layers, z_i is the average

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depth of sampled layer i, and a is the number of depth layers sampled. For each survey, the ping-weighted average of PD from the five transects was calculated.

Simultaneously to the hydroacoustic surveys, zooplankton were sampled with a conical closing plankton net (mesh size 90 µm, opening 0.02 m^2, length 1.2 m) at a fixed location near the deepest point (69 m) in the central basin of Lake Stechlin (Fig. 1). Triplicate hauls were taken from five water depths (0–10, 10–20, 20–30, 30–40, and 40 m to the bottom). The three hauls per depth layer were subsequently pooled and fixed in sugar–formaldehyde, and species were identified and enumerated in the laboratory from at least three smaller subsamples. Zooplankton were categorized into four groups, namely daphnids (*Daphnia cucullata*, *D. hyalina*), small cladocerans (*Bosmina coregoni*, *Bosmina longirostris*, *Alonella nana*, *Ceriodaphnia quadrangula*, *Acroperus harpae*, *Alona quadrangula*, *Disparalona rostrata*, *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Pleuroxus uncinatus*, *Polyphemus pediculus*, *Canthocamptus staphylinus*), adult copepods (*Eudiaptomus gracilis*, *Eurytemora lacustris*, *Cyclops strenuus*, *Thermocyclops oithonoides*, *Mesocyclops leukarti*, *Megacyclops viridis*, *Heterocope appendiculata*, *Diacyclops bicuspidatus*), and immature copepods (copepodit and nauplii stages). Group-specific population depths were calculated similar to the procedure described for fish.

Water temperatures were continuously recorded every 30 min by temperature loggers fixed close to the deepest point of the lake at the surface and at 2 m depth intervals down to 20 m, with an additional logger placed nearby at a depth of 30 m. Water temperatures in the same layers were not substantially different between day and night (maximum difference 0.9 °C at the surface during some summer days). Accordingly, daily average temperatures for the lake were calculated from the 48 recordings per day over all 12 depths of measurements. Other abiotic variables (oxygen concentration (mg·L^{-1}), pH value, and Secchi depth (m)) were determined at 5 m depth intervals close to the deepest point of the lake during routine surveys conducted monthly (October to April) or biweekly (May to September). For oxygen concentrations and pH values, both a vertical average and a gradient (maximum – minimum values over the depth intervals) were calculated per sampling date.

Statistics

Comparisons of lake-wide fish and zooplankton densities over the diel, seasonal, horizontal, and vertical sampling scales were not the purpose of this study and are described elsewhere based on earlier surveys in Lake Stechlin (Mehner et al. 2005*b*). Therefore, here only the average densities and population depths of the three fish groups were compared between day and night and over the 10 sampling months. To achieve normal distribution and homoscedasticity, Box–Cox transformations (Sokal and Rohlf 1995) were applied to fish densities and population depths. Natural-log transformation ($\lambda = 0$) resulted in normality (Kolmogorov–Smirnov tests, $P > 0.087$) and homoscedasticity (Brown–Forsythe tests, $P > 0.81$) for volumetric densities, whereas a Box–Cox transformation with $\lambda = 0.4$ (Rundom BC 1.0, freely available from http://pjadw.tripod.com/soft.htm) achieved normality ($P > 0.16$) and homoscedasticity ($P > 0.23$) for population depths. Furthermore, the ping-weighted mean densities and population depths per fish group and month were not serially autocorrelated at lags 1 or 2 (all $r < 0.48$, $P > 0.09$). Densities and population depths could be calculated for both small and large coregonids from all transects sampled (total $N = 5$ transects × 10 months × 2 diel samplings = 100 each). In contrast, echoes from predator-like fishes were missing at 14 transects (4 in April, 5 in May, 2 in June, 1 in July, 2 in August; in total four daytime values, 10 nighttime values) so that the total number of measurements from all three fish groups included was 286. The missing cells were excluded from analyses. For both fish densities and population depths, an univariate three-way analysis of variance (ANOVA) was applied (type III sums of squares to account for nonorthogonal design) by including fish size GROUP (small, large, predators), DIEL (day/night), and MONTH (March to December) as the main effects, and all possible two-way and three-way interactions. If interaction effects were significant, overall statements for main effects were considered to have little meaning (Sokal and Rohlf 1995, p. 336).

Correlations were calculated between the monthly population depths of small or large fish and the abiotic variables water temperature, pH value, oxygen concentration, and Secchi depth. In addition, the experienced water temperature at the population depths and the temperature difference experienced during diel vertical migrations (temperature at nighttime population depth minus hypolimnetic temperature below 30 m depth) were included in correlation analyses. It was assumed that depth distribution of fish was correlated to abiotic variables (in particular the water temperature) if the bioenergetics efficiency hypothesis of DVM applied. Although water temperatures were measured at the dates of hydroacoustic samplings, all other variables were taken from measurements conducted close to the dates of fish samplings (21 March, 9 April, 26 May, 9 June, 26 July, 11 August, 21 September, 19 October, 10 November, 6 December 2005). This temporal deviation most likely did not produce substantial bias because of the rather continuous succession of the abiotic conditions over the sampling period (see Results).

Furthermore, correlations were calculated between population depths of fish and the average population depths of the four zooplankton groups to elucidate whether fish depth distribution corresponded to the depth distribution of zooplankton (feeding opportunity hypothesis). The average population depth of the predator-like fish group was included to test whether population depth of coregonids was negatively correlated to depth of potential predators (predator avoidance hypothesis). Finally, the mean target strength of all echoes reflecting either small or large fish per survey was correlated to the population depths of fish to test whether the seasonal variability in population depth was mainly attributable to changes in average fish size due to recruitment. All variables ($N = 10$ in each case except for nighttime predator depth where $N = 9$) were normally distributed (Kolmogorov–Smirnov test, $Z > 1.21$, $P > 0.110$) such that Pearson's linear correlation coefficients (r) were calculated. We did not correct the significance level from $\alpha = 0.05$ to a lower, table-wide value by a sequential Bonferroni procedure according to recent discussions that the chance of many weakly signifi-

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Table 1. Results of univariate three-way analyses of variance (ANOVAs) on natural log transformed volumetric densities (individuals·1000 m^{-3}) or Box–Cox transformed ($\lambda = 0.4$) population depths (m) of three size groups of fish from five hydroacoustic transects per survey at Lake Stechlin in 2005 (total $N = 286$).

	Sums of squares	*df*	*F*	*P*
Volumetric density				
Model	1 319.2	58	25.4	<0.0001
Constant	33.5	1	37.4	<0.0001
DIEL	200.1	1	223.5	<0.0001
MONTH	79.5	9	9.86	<0.0001
GROUP	821.9	2	458.8	<0.0001
DIEL × MONTH	22.7	9	2.81	0.004
DIEL × GROUP	53.0	2	29.6	<0.0001
MONTH × GROUP	45.9	18	2.85	<0.0001
DIEL × MONTH × GROUP	41.2	17	2.70	<0.0001
Error	203.3	227		
Corrected total	1 522.6	285		
Population depth				
Model	437.1	58	10.3	<0.0001
Constant	13 205.0	1	18 104.9	<0.0001
DIEL	263.5	1	361.3	<0.0001
MONTH	46.3	9	7.05	<0.0001
GROUP	3.5	2	2.38	0.095
DIEL × MONTH	12.6	9	1.92	0.050
DIEL × GROUP	13.4	2	9.18	<0.0001
MONTH × GROUP	40.9	18	3.11	<0.0001
DIEL × MONTH × GROUP	55.6	17	4.48	<0.0001
Error	165.6	227		
Corrected total	602.7	285		

Note: The main effects and their two-way and three-way interactions tested were DIEL (day/night), MONTH (10 months between March and December 2005), and size GROUP of fish (small coregonids, large coregonids, predator-like fishes).

cant correlations being spurious is extremely improbable (Moran 2003).

All calculations were performed by SPSS 9.0 (SPSS Inc. 1999).

Results

Average ping-weighted volumetric densities of the three fish groups substantially varied between day and night and between the 10 sampling months (Fig. 2). Annual average densities were lower for small (6.54 individuals·1000 m^{-3}) than for large (10.58 individuals·1000 m^{-3}) coregonids at night, whereas the density of predator-like fishes was about 30–50 times lower (0.22 individuals·1000 m^{-3}). Total fish density was equivalent to about 693 000 fish·km^{-2} if an average depth of the five transects of 40 m is considered. Densities of small and large coregonids during daytime surveys were always lower than during nighttime recordings (Fig. 2). Coregonid densities peaked in July (Fig. 2*a*, small fish) or August (Fig. 2*b*, large fish), whereas highest densities of predator-like fishes were found in March (Fig. 2*c*). All two-way (DIEL × MONTH, DIEL × GROUP, MONTH × GROUP) and three-way (DIEL × MONTH × GROUP) interaction effects were significant in the ANOVA of natural log transformed densities, indicating that the temporal differences between the months and between day and night were variably expressed in the densities of the three fish groups (Table 1).

The ping-weighted average population depths of small or large coregonids showed little variability between the five transects per survey during the night compared with the higher differences between transects found during daytime surveys (Fig. 3). The annual average population depth of small coregonids at night (18.5 m) was slightly lower than that calculated for large coregonids (22.2 m) or predator-like fishes (24.5 m). Nighttime population depths were reduced from March to the summer months (June to August) and were located again deeper from September to November (Figs. 3*a*, 3*b*). Population depths during daytime did not follow a regular pattern, but fish were always found deeper during the day than at night. The estimated average diel migration amplitudes were 18.7 m (range 9.2–28.2 m) in small coregonids and 14.3 m (range 7.0–25.9 m) in large coregonids. In predator-like fishes, nighttime population depth was lowest in April and June, but fish moved deeper during the summer (Fig. 3*c*). In some months, the population depth was found at lower depths during daytime than at night. The annual average migration amplitude of predator-like fishes was 12.4 m (range –5.4 to 31.0 m). In the ANOVA of Box–Cox transformed population depths, the MONTH × GROUP, DIEL × GROUP, and DIEL × MONTH × GROUP interactions were significant, indicating that the differences in population depth between months or day and night were not identical in the three fish groups (Table 1). However, the DIEL × MONTH interaction was only weakly

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Fig. 2. Average volumetric densities (individuals·1000 m^{-3} ± standard deviation, SD) of fish in Lake Stechlin, as estimated from five hydroacoustics transects during day (open circles) or night (solid circles) over 10 months in 2005. Fish size groups displayed: (*a*) small (2.5–8 cm length) and (*b*) large (8–24 cm length) coregonids and (*c*) predator-like fishes (24–45 cm length). Predator density was zero during nighttime in May.

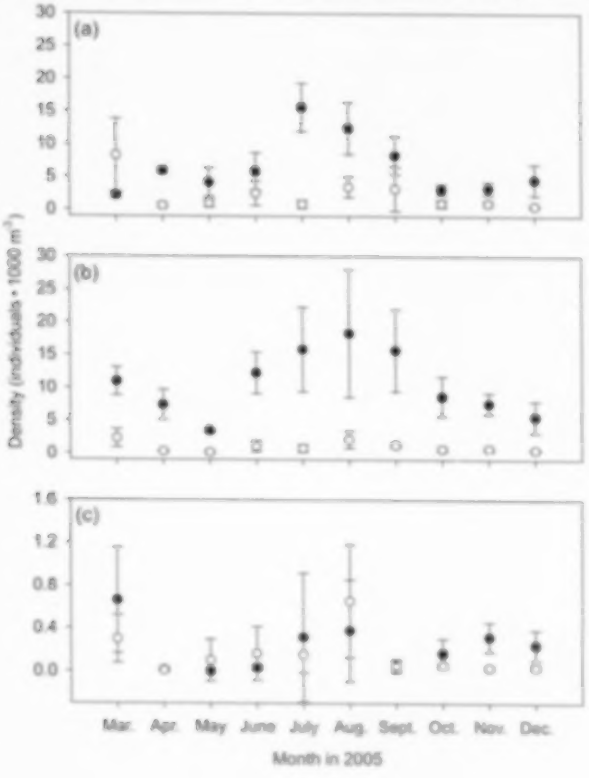
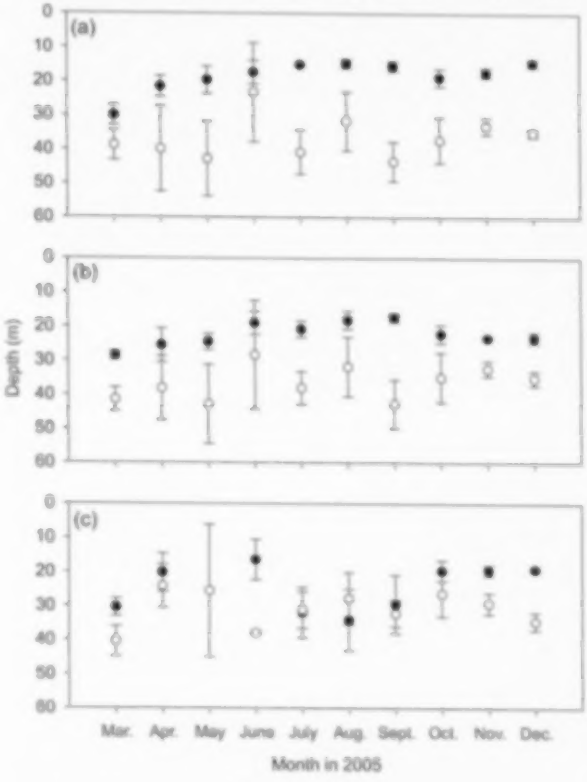


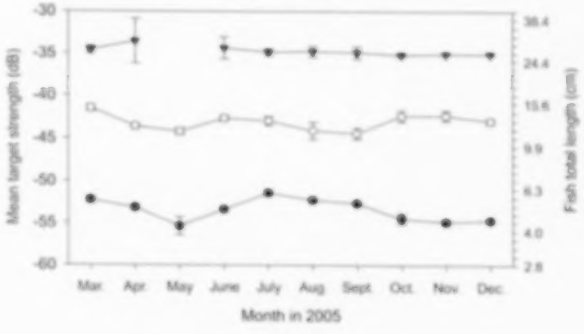
Fig. 3. Average population depth (in metres ± standard deviation, SD) of fish in Lake Stechlin, as estimated from five hydroacoustics transects during day (open circles) or night (solid circles) over 10 months in 2005. Fish size groups displayed: (*a*) small (2.5–8 cm length) and (*b*) large (8–24 cm length) coregonids and (*c*) predator-like fishes (24–45 cm length). No data on nighttime depth of predators are available during May.



significant ($P \approx 0.05$). This means that as an overall tendency, the differences in depth distributions between day and night were stable over all sampling months, thus reflecting that the coregonids performed a regular DVM without seasonal interruption. However, because of the continuously substantially lower volumetric densities and the much stronger intertransect variability of both densities and population depths during daytime surveys compared with nighttime surveys, we considered the daytime estimates to be less reliable and focused further correlation calculations exclusively on the nighttime data.

The mean TS per fish group varied little between the five transects per nighttime survey but showed some seasonal fluctuations, presumably owing to variable contributions of newly recruited fish (Fig. 4). In zooplankton, the population depths did not substantially differ between day and night during the majority of the 10 sampling months (Fig. 5). Diel differences in population depths were most pronounced in immature and adult copepods. However, there were no continuous migration patterns because the population depth shifted irregularly upwards or downwards between day and night over the 10 months in all groups. For most of the zooplankton, the diel average population depth shifted upwards

Fig. 4. Average target strengths (in dB ± standard deviation, SD) of fish in Lake Stechlin, as estimated from five hydroacoustics transects during day or night over 10 months in 2005. Fish size groups displayed: small (2.5–8 cm length) coregonids, solid circles; large (8–24 cm length) coregonids, open circles; predator-like fishes (24–45 cm length), solid triangles.



in summer and was situated in deeper layers in the early spring and late autumn (Fig. 5). Accordingly, the majority of the zooplankton was always found 10–15 m higher in the

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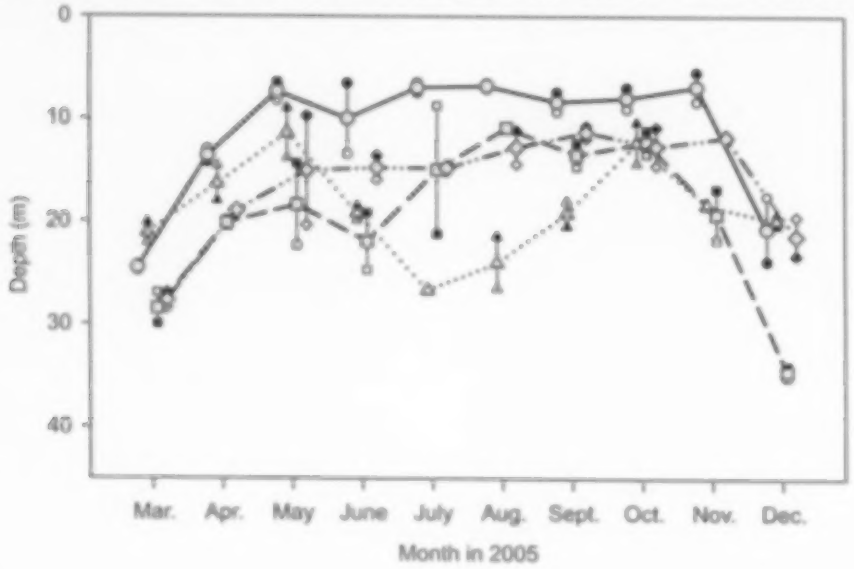
Fig. 5. Diel average population depths (m) of four zooplankton groups (*Daphnia* spp., solid line and circles; small cladocerans, dotted line and triangles; adult copepods, dashed line and squares; immature copepods, dashed–dotted line and diamonds) in Lake Stechlin during day or night over 10 months in 2005. The diel migration amplitudes are indicated by the whiskers; open symbols indicate daytime depth, solid symbols indicate nighttime depth. The symbols are slightly staggered along the *x* axis to improve readability.



water column than the coregonids during daytime, whereas there was a closer spatial overlap during nighttime.

Annual succession of water temperature was highly divergent between surface and hypolimnetic water layers (Fig. 6*a*). The highest temperature difference between the surface and the 30 m depth was recorded at about 17 °C in July (Fig. 6*a*). The steepest temperature gradients were always found during the stratification period around the thermocline between water depths of 8 and 14 m. Secchi depth varied between 6.8 and 11.2 m (Fig. 6*b*). The average oxygen concentration, estimated over the water column, declined over the season and reached its lowest value in December (7.26 mg·L^{-1}; Fig. 6*c*). Simultaneously, the difference between the highest and the lowest concentrations increased such that the vertical oxygen gradient was steepest at the end of the year (Fig. 6*c*), but low concentrations between 3 and 4 mg·L^{-1} were recorded only in depths of more than 60 m between the end of November and December 2005. The average pH values only slightly declined from 8.5 to 7.7 over the year, whereas the differences between maximum and minimum values, indicating a vertical gradient, were a bit higher during summer than in the other periods (Fig. 6*d*).

The nighttime population depths of both small and large coregonids were not correlated to population depths of either predators or the four zooplankton groups, except for a weakly significant correlation between depths of large fish and immature copepods (Table 2). Furthermore, the seasonally varying target strengths of fish did not correspond to the nighttime population depths.

However, significant correlations were calculated between some abiotic variables and depths of fishes. In addition to calculating an average temperature over the full vertical gradient (0–30 m), averages were also calculated over the surface (0–6 m) and over the hypolimnetic layers (16–30 m) according to similar temperature trends in these water layers (Fig. 6*a*). The four layers in between (8, 10, 12, and 14 m) were tested separately. Population depths of both small and large fish were negatively correlated to temperatures in the surface layer and at 8, 12, and 14 m and to the average temperature over the full depth range (Table 2). Hypolimnetic water temperature corresponded to population depths of small fish only, whereas temperatures at 10 m corresponded to depths of large fish only. In total, the average temperature over 0–30 m best corresponded to population depths of small and large coregonids (average of the two coefficients $r = -0.805$), thus indicating that fish occupied lower water depths during warmer months (Fig. 7). Accordingly, the experienced water temperature at the population depth at night was significantly negatively correlated to population depth for both small and large coregonids. Furthermore, the temperature difference experienced during the migration from daytime to nighttime population depths was negatively correlated to the nighttime depth of large fish (Table 2).

Secchi depths and fish depths were not correlated. However, the population depths of small fish were positively correlated to average oxygen concentrations and pH values and negatively correlated to the difference between maximum and minimum pH values. The latter variable was negatively correlated also to the depth of large fish. It has to be noted, however, that all these variables were similarly strongly correlated to the hypolimnetic water temperature (all $N = 10$; oxygen concentration, $r = -0.89$, $P = 0.0006$; pH, $r = -0.90$, $P = 0.0003$; pH gradient, $r = 0.80$, $P = 0.005$). This indicates

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Fig. 6. Overview on seasonal succession of abiotic conditions in Lake Stechlin between March and December 2005. Data displayed: (*a*) water temperature (°C) in 12 depths; (*b*) transparency, measured as Secchi depth (m); (*c*) average oxygen concentration (mg·L^{-1}) over the full vertical range (solid circles) and vertical gradient in oxygen concentration (maximum – minimum; open circles); and (*d*) average pH value over the full vertical range (solid circles) and vertical gradient in pH (maximum – minimum; open circles).

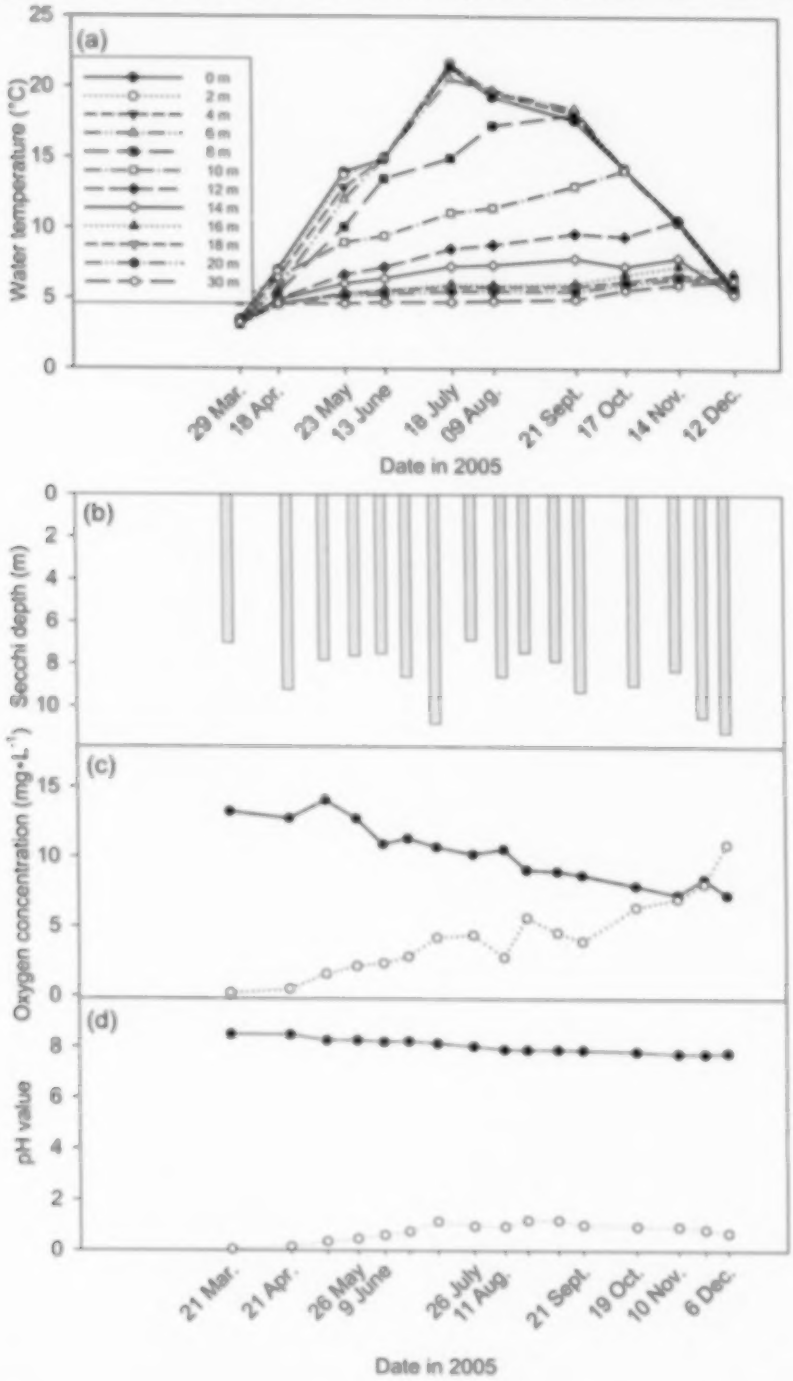

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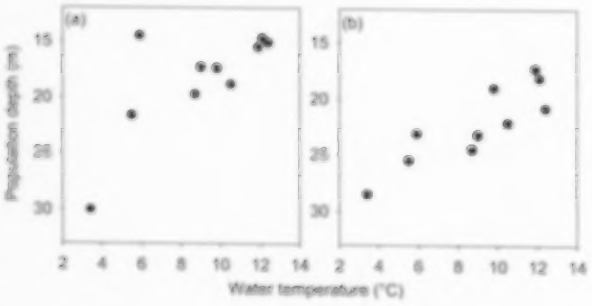
Table 2. Overview on linear correlations (Pearson's *r*) between average population depths (m) of small or large coregonids during nighttime hydroacoustic surveys in Lake Stechlin over 10 months in 2005, and target strength of this fish group, population depths of predators and four zooplankton prey groups (m), and 14 abiotic variables ($N = 10$ in all cases except for predator depth where $N = 9$).

Variables	Population depth (m)	
	Small coregonids	Large coregonids
Target strength (dB)	0.088	0.52
Population depth of predators (m)	0.047	–0.18
Population depth of daphnids (m)	0.50	0.62
Population depth of small cladocerans (m)	–0.22	–0.27
Population depth of adult copepods (m)	0.33	0.56
Population depth of immature copepods (m)	0.58	**0.65** *
Average water temperature at 0–30 m (°C)	**–0.74** *	**–0.87** **
Average water temperature at 0–6 m (°C)	**–0.66** *	**–0.83** *
Water temperature at 8 m (°C)	**–0.66** *	**–0.91** ***
Water temperature at 10 m (°C)	–0.53	**–0.71** *
Water temperature at 12 m (°C)	**–0.68** *	**–0.70** *
Water temperature at 14 m (°C)	**–0.78** **	**–0.79** **
Average water temperature at 16–30 m (°C)	**–0.84** **	–0.52
Experienced temperature at population depth (°C)	**–0.83** **	**–0.64** *
Difference in experienced temperature between day and night	–0.36	**–0.83** **
Average oxygen concentration at 0–69 m ($mg \cdot L^{-1}$)	**0.65** *	0.44
Gradient in oxygen concentration (maximum – minimum)	–0.60	–0.20
Average pH value at 0–69 m	**0.75** *	0.57
Gradient in pH (maximum – minimum)	**–0.82** **	**–0.79** **
Secchi depth (m)	–0.41	–0.14

Note: Significant correlations are given in bold and *P* values are indicated by asterisks (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

Fig. 7. Scatter plots of average water temperature at 0–30 m depth vs. population depth (m) at night of (*a*) small (2.5–8 cm length) or (*b*) large (8–24 cm length) coregonids in Lake Stechlin over 10 months in 2005.



that water temperature, oxygen concentration, and pH were strongly coupled in the layers below the thermocline in Lake Stechlin.

Discussion

Our data show that both small (young-of-the-year) and large (juvenile and adult) coregonids in Lake Stechlin exhibit diel vertical migrations with an average amplitude over all months of about 14–19 m. Size-group specific differences in residence depths and migration amplitudes were relatively low. The overall migration pattern of the coregonids varied little over a full seasonal cycle, irrespective of the documented changes in population depths of both food resources (zooplankton groups) and potential fish predators. Consequently, from our data there is only weak support for the predator avoidance or feeding opportunity hypotheses in the DVM of coregonids in Lake Stechlin. In contrast, there was a high number of strongly significant negative correlations between water temperatures in several layers and other interrelated abiotic factors on the one hand and average depths of the fish populations at night on the other hand. This modification of nighttime population depths by temperature might support the bioenergetics efficiency hypothesis of DVM. A similar temperature-dependent distribution pattern was found for zooplankton in several deep lakes (Burns and Mitchell 1980; Winder et al. 2003; Thackeray et al. 2006).

The fish densities estimated by hydroacoustics during daytime were continuously lower than the recordings at night. Furthermore, the estimated population depths of the fish groups were highly variable between the five transects per survey during daytime but showed little variability during nighttime surveys. Both patterns are attributable to the differing dispersal of the coregonids between day and night. During daytime, fish aggregate in large schools at water depths below about 40 m. In all areas where the lake is shallower, fish hide directly at the bottom in the "dead zone" such that the strong bottom echo superposes the fish echoes (see Axenrot et al. 2004). During the night, fish ascend into shallower water layers and disperse more evenly. Accordingly, the number of SEDs increases substantially, and the average population depths can be estimated with higher precision. Thus, whereas estimates of fish population depths

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during nighttime were reliable, daytime recordings have to be treated with caution, as the calculations of population depth are based only on a limited part of the entire population. A similar improvement in precision of hydroacoustic recordings during the night as compared with daytime surveys has been reported from other studies in which diel migrations of fish were tracked (Appenzeller and Leggett 1992; Axenrot et al. 2004). In contrast, it is highly unlikely that the density differences between day and night were attributable to horizontal migrations out of the study area as earlier analyses revealed little fish density differences between the four main basins of Lake Stechlin (Mehner et al. 2005*b*).

Methodological difficulties of hydroacoustic recordings may have also influenced the estimates of density and depth distribution of the predator-like fishes. SEDs >–36 dB, i.e., fish bigger than about 25 cm length, were relatively scarce. The relative density of predators in that size range was estimated with 1.27% of total pelagic fish density, based on the annual averages from the nighttime surveys. Perch, a day-active cruising predator (Bergman 1988) reported to feed on vendace (Huusko et al. 1996; Heikinheimo 2001), is present also in Lake Stechlin (Anwand et al. 2003). However, fishing data from Lake Stechlin revealed an only occasional occurrence of perch in the pelagic area. The relative proportion by numbers of perch was 0.8% during a standardized fishing with 13 pelagic gillnets in Lake Stechlin in 2002 (see Mehner et al. 2005*a*). Regular fishing by gillnets in the pelagic area of Lake Stechlin over 8 months in 2000 caught only 12 perch among the total of 1871 fish (0.6%) (Mehner and Schulz 2002). Several hauls by a pelagic midwater trawl did not catch any perch in 2002 and 2003 (Mehner 2006). Likewise, in a total of 80 hauls with the same trawl in 10–35 m depth completed concurrently with the hydroacoustic estimates in Lake Stechlin during day and night in 2005, no perch was caught at all (Helland et al. 2007). In none of the pelagic fishing surveys was any other piscivorous species caught. Accordingly, it is very likely that the hydroacoustic data overestimated the pelagic predator densities.

One possible reason was found while thoroughly inspecting the hydroacoustic files in which SEDs >–36 dB were found. Predator-like echoes were almost always located within the densest parts of large schools of coregonids. In this case, superimposed echoes from two fish near to each other may have a combined energy more than that coming from one fish, resulting in the indicated target strengths being too high (Simmonds and MacLennan 2005). If all of these suspicious detections of predators were excluded, the predator densities would amount to less than 0.1% of the total densities estimated for the coregonids. More recently, fish-eating birds were considered as a major source of fish mortality (Steinmetz et al. 2003). However, the number of cormorants (*Phalacrocorax* spp.) did not exceed 20 on any of the sampling occasions, and great crested grebes (*Podiceps cristatus*) were likewise not abundant. This overall very low predator density let us conclude that the real risk of being prey in the illuminated layers was not a main factor triggering the occurrence of vendace and Fontane cisco in the dark hypolimnetic layers during daytime. The low risk of encountering predatory fish in the upper water layers was furthermore indicated by the estimated population depths of predator-like fishes, which were situated outside of the illuminated zone below 25 m during daytime in all months. Accordingly, population depths of predators were not at all correlated to the coregonid population depths.

Feeding opportunity was likewise an inappropriate explanation for the DVM in coregonids. Population depths of zooplankton were seasonally variable but relatively invariant between day and night. This distribution pattern corroborates earlier findings that migration amplitudes of the zooplankton in Lake Stechlin are small (Kasprzak and Schwabe 1987). Levy (1990) argued that DVM in zooplankton might be linked to the presence or absence of diel migrations in coldwater pelagic planktivorous fish. He found that zooplankton distribution was vertically invariant in those lakes in which juvenile sockeye salmon (*Oncorhynchus nerka*) undertook diel vertical migrations. Accordingly, a zooplankton DVM is not expected in Lake Stechlin because of the strong DVM of the coregonids. The zooplankton groups concentrated in water layers above the preferred water depth of the coregonids during daytime, thus preventing strong habitat overlap with and predation mortality by the planktivores. In turn, the feeding opportunities for fish were good only during nighttime when the coregonids had ascended into those layers where zooplankton groups persisted. The following downward migration during dawn is, however, inefficient as only individuals that remained in the upper layers over all the diel cycle would maximize their feeding rates. Therefore, if food availability alone determined the depth distribution of coregonids, then daytime occurrence of fish below the layers where zooplankton occur would be a maladaptive strategy.

The strong correlation between population depths of coregonids during nighttime and the average water temperature seems to support the bioenergetics efficiency hypothesis of DVM. Two contradicting mechanisms, postfeeding and prefeeding thermotaxis, have been described. Larval Bear Lake sculpins (*Cottus extensus*) were found to speed up their postfeeding digestion rate by migrating into warmer water where the higher temperatures allowed the fish to feed and grow three times faster than if they had remained in the cold layers close to the bottom (Wurtsbaugh and Neverman 1988). In contrast, if fish feed intensively in warm, food-rich layers during the night but save energy by migrating to colder water during the day, then their total scope for growth likewise may be higher. Bevelhimer and Adams (1993) modeled the bioenergetics efficiency of DVM in juvenile kokanee salmon (*Oncorhynchus nerka*). They found that when the preferred temperature and optimum prey densities were spatially separated, vertical migrations could result in greater growth compared with no migration. The general rule developed for DVM from the model was to feed where net energy is maximized and then reside when not feeding where energetic costs are minimized and food is digested to the point that consumption during the next feeding period is not limited by the stomach capacity (Bevelhimer and Adams 1993). Recently, a combination of empirical observations and experimental approaches confirmed that adult male dogfish (*Scyliorhinus canicula*) could lower daily energy costs by just over 4% by adopting a "hunt warm – rest cool" strategy (Sims et al. 2006). The gain in efficiency will probably increase with the temperature difference between the two

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layers, thus explaining why coregonids shifted their nighttime population depth upwards during warmer months. The experienced temperatures in these depths did not exceed 7.4 °C, which is metabolically not critical for coregonids. Experimental data suggest that adult vendace avoid water temperature above 18 °C, although their lethal temperature is even 23–24 °C (Hamrin 1986). The final temperature preferendum of juvenile vendace is also higher than 7.4 °C and was determined at about 16 °C in summer and 12 °C in winter (Tapaninen et al. 1998).

Bioenergetics explanations of DVM have additionally to consider the costs of the migration itself. Earlier models of DVM have assumed no costs (Clark and Levy 1988), or it was assumed that migration costs are substantial, although reliable estimates were not available (Bevelhimer and Adams 1993). Using a bioenergetics model of buoyancy regulation in adult Atlantic cod (*Gadus morhua*), it was shown that regulation of swimbladder volume during DVM is energetically cheap but slow (Strand et al. 2005). The application of the model to in situ observations of vertical positions of living cod revealed average energy consumption rates of about 0.28 $J \cdot kg^{-1} \cdot s^{-1}$, with the additional costs of vertical migrations being about 50% of the standard metabolic rate (Strand et al. 2005, their fig. 7*c*). If the rate of 0.28 $J \cdot kg^{-1} \cdot s^{-1}$ is applied to a 10 g vendace, costs of DVM would amount to about 242 J in 24 h, equivalent to about 0.5% of the body energy content of this fish. In a strict sense, the model, which was developed for the physoclist cod, cannot be applied to the physostome vendace. However, the rough estimate shows that costs of DVM are probably relatively low compared with other components of bioenergetics budgets. Accordingly, to make DVM an efficient strategy, the metabolic advantage gained by the migration between the layers with differing temperature can be expected to exceed the pure migration costs.

However, the bioenergetics efficiency hypothesis fails to explain why DVM of coregonids was stable over all sampling seasons. During all those months when the lake is not stratified, the lacking temperature gradient prevents improvements of bioenergetics efficiency by migrations. Lake Stechlin was completely isothermal in March 2005, and temperature differences between surface and bottom were less than 2.5 °C in April and December 2005. Nevertheless, the coregonids also migrated in these months, and no temporal interruption of DVM was observed. Similarly, a vendace DVM was also documented in the shallow Lake Pyhäjärvi (Finland), which did not show thermal stratification during the study period (Sydänoja et al. 1995). Consequently, the water temperature (or the interrelated oxygen concentrations and pH values) obviously modified the migration range but did not induce or stop the migration as such.

The seasonal stability of the migration patterns suggests that the DVM of coregonids in Lake Stechlin is, at least in part, a genetically fixed behavioral strategy. This would distinguish the DVM of the coregonids from other adaptive habitat use patterns described for fish. DVM in juvenile sockeye salmon was considered to be adaptive and inducible as fish matched the antipredation window against predatory salmonids during their ascent and descent in dusk and dawn (Clark and Levy 1988; Scheuerell and Schindler 2003). Recent studies on lake ciscoes (*Coregonus* spp.) in the North American Lake Superior likewise indicated that diel variability in predation risk by siscowet (*Salvelinus namaycush siscowet*), controlled by changing light levels, modified the diel vertical distribution of cisco populations (Hrabik et al. 2006; Jensen et al. 2006). Similarly, horizontal migrations of fish between littoral and pelagic sites in lakes, or timing of ontogenetic habitat shifts, can be highly flexible and inducible by varying diet profitabilities and predator densities (Werner et al. 1983; Byström et al. 2003; Hölker and Mehner 2005). In contrast, a genetically fixed behavior was suggested to explain the early offshore migration of perch larvae (Post and McQueen 1988; Byström et al. 2003), which occurs in almost all perch populations studied irrespective of whether the predation risk in the pelagic area was high or low. In a similar way, DVM in vendace is reported from a wide range of lakes, although mean depths, water temperatures, diet availabilities, and predator densities differ substantially between these locations (Dembinski 1971; Hamrin 1986; Sydänoja et al. 1995).

Recently, the nocturnal feeding of the small benthivorous stone loach (*Barbatula barbatula*) was interpreted as a fixed behavioral strategy (Fischer 2004). The stone loach did not adopt daytime feeding, even when there was no acute daytime predation risk and the fish were severely starving. Fischer (2004) thus suggests that the fish use the anticipated rather than the observed predation risk, a strategy that may have primacy if an animal has imperfect knowledge about its stochastic environment (Bouskila and Blumstein 1992). As a consequence, the animal does not quantitatively weigh mortality versus growth rates to choose the optimal habitat but favors safety over food and frequently maintains predator-avoidance behavior even in the absence of continued threat (Hampton 2004). Accordingly, the stability of the DVM pattern in the coregonids in Lake Stechlin may be interpreted as anticipation of predation risk by visual predators in the illuminated upper water layers during daytime, although the real predation threat was negligible. Blumstein (2006) assumes that in species that have experienced a multiple predator environment in former times, antipredator behavior will persist despite the loss of one or more predator species. He suggests that pleiotropy and (or) linkage seem to be reasonable mechanisms explaining persistence of antipredator behavior. Pleiotropy occurs when a single gene influences multiple phenotypic traits; thus, elements of antipredator behavior may have a function in nonpredatory situations. Linkage means that genes influencing the expression of antipredator behavior do not assort independently. In such cases, the underlying genetic basis of antipredator behavior has, by pleiotropy or linkage, become a functional package.

Accordingly, a heritable basis of the vertical migration behavior in the coregonids should be expected to exist. There is experimental evidence that the average swimming depth in lake whitefish (*Coregonus clupeaformis*) ecotypes is, at least in part, a heritable trait. Rogers et al. (2002) found that the dwarf ecotype preferred the highest position in the water column, whereas the normal-sized ecotype preferred deeper waters. Hybrid crosses showed an intermediate swimming depth, leading to the conclusion that the genetic basis of depth preference consists of an additive component. In

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Daphnia, the coexistence of genetically different, migrating and nonmigrating clones was reported as a source of observed variability in vertical migration patterns (Weider 1984; De Meester et al. 1995). No such studies are available for fish. However, if one considers that regular short-term changes over temperature or pressure gradients require substantial physiological adaptations (e.g., Stensholt et al. 2002; Speers-Roesch et al. 2004), then it seems to be plausible to assume that vertical migrations have at least a heritable component also in fish.

In conclusion, we suggest that the DVM of coregonids in Lake Stechlin is not an inducible phenotypic trait as has been suggested for most of the zooplankton DVM (Hays 2003). Instead, it seems to be a fixed behavior adapted to minimize the potential predation risk by predators stochastically occurring in the illuminated upper layers, e.g., perch or fish-feeding birds. As long as the net energy gain of this behavioral trait is positive, allowing the fish to grow, there is no selection pressure towards a more efficient strategy. The inefficient DVM of the coregonids in Lake Stechlin is not a disadvantage to fitness as there are no other planktivorous species in the pelagic area that could outcompete the coregonids by staying continuously in the layers where zooplankton concentrate. Levy (1990) speculated that a change in DVM patterns of juvenile kokanee salmon might be created if kokanee has to compete with coexisting three-spined sticklebacks (*Gasterosteus aculeatus*). Therefore, the interdependencies of changed habitat profitabilities due to competition, the DVM patterns in fish, and their genetic fixation need to be explored in more detail.

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Zooplankton community response to experimental acidification in boreal shield lakes with different ecological histories

Alison M. Derry and Shelley E. Arnott

Abstract: Community responses to acidification and recovery of boreal lakes are poorly understood, particularly after several years of recovered lake-water pH (pH ≥ 6.0). We tested if zooplankton communities in two circumneutral lakes with different acidification histories were adapted to historical lake-water pH with a reciprocal transplant field enclosure experiment. A second objective was to assess the influence of local environments on zooplankton survival and abundance. Differences in acid tolerance could be detected in some zooplankton among the two lakes with different acidification histories — zooplankton from acid-recovering Carlyle Lake, recovered to pH ≥ 6.0 for 6 years were more speciose and maintained higher total abundance at pH 4.8 than the community from a buffered lake. The zooplankton community in this historically acidified lake was comprised of two dominant species with acid-adaptable tolerances, *Holopedium gibberum* and *Leptodiaptomus minutus*. High establishment of transplanted zooplankton in our experiment has important implications for the recovery of zooplankton communities because it suggests that local conditions are suitable for most species in acid-recovering lakes with pH ≥ 6.0 and that other factors such as dispersal limitation and biotic interactions may be impeding recovery.

Résumé : Dans les lacs boréaux, les réactions de la communauté à l'acidification et sa récupération restent mal comprises, particulièrement lorsque le pH du lac a été rétabli (pH ≥ 6,0) depuis plusieurs années. Une expérience d'enclos en nature avec transfert réciproque nous a servi à vérifier si les communautés zooplanctoniques dans deux lacs à pH près de la neutralité, mais avec des histoires d'acidification différentes, se sont adaptées au pH historique des lacs. Un second objectif est d'évaluer l'influence des environnements locaux sur la survie et l'abondance du zooplancton. Il existe dans ces deux lacs à histoire d'acidification distincte des différences décelables de tolérance à l'acidité chez certains organismes du zooplancton : le zooplancton du lac Carlyle, qui a retrouvé un pH ≥ 6,0 depuis 6 ans, est plus riche en espèces et maintient des densités totales plus grandes à un pH de 4,8 qu'une communauté provenant d'un lac tamponné. La communauté zooplanctonique dans ce lac qui a subi une acidification dans le passé comprend deux espèces dominantes, *Holopedium gibberum* et *Leptodiaptomus minutus*, qui possèdent des tolérances adaptables à l'acidité. La forte colonisation du zooplancton transplanté dans notre expérience a des implications importantes sur le rétablissement des communautés zooplanctoniques : elle indique, en effet, que les conditions locales sont adéquates pour la plupart des espèces dans les lacs en récupération à pH ≥ 6,0 et ce que sont peut-être d'autres facteurs, tels que les contraintes de la dispersion et les interactions biotiques, qui nuisent à la récupération.

[Traduit par la Rédaction]

Introduction

Acid rain has been a serious environmental problem in North America and Europe for several decades (Schindler 1988) and is emerging as a growing threat in other parts of the world where there is rapid industrialization, e.g., China (Larssen et al. 2006). Acid deposition has damaging effects on freshwater ecosystems, causing loss of fish and invertebrate populations (Minns et al. 1990), reduced biological diversity (Beamish and Harvey 1972; Confer et al. 1983), loss of ecosystem function, particularly at higher trophic levels (Fischer et al. 2001*a*; Vinebrooke et al. 2003), and increased sensitivity to the impacts of multiple stressors (Frost et al. (1999). Evolutionary implications of lake acidification have been less studied but include shifts in acid tolerances in copepods (Fischer et al. 2001*b*; Derry and Arnott 2007), as well as community-level responses in crustacean zooplankton (Fischer et al. 2001*b*).

Legislation was introduced in North America and Europe that reduced acidic atmospheric deposition of sulphur during the 1980s and 1990s, and subsequently, many lakes damaged by acid precipitation are starting to recover chemically (Stoddard et al. 1999; Jeffries et al. 2000). Research has shown time lags in the re-establishment of predisturbance aquatic communities following chemical lake-water recovery (Keller et al. 2002; Holt and Yan 2003; Frost et al. 2006). Local (pH, community resistance, egg bank recruitment, invertebrate predation) and regional (dispersal) factors may

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limit the re-establishment of zooplankton species diversity in acid-recovering lakes (Arnott et al. 2001, 2006; Binks et al. 2005). A relatively unexplored factor in community recovery following disturbance is the adaptive shift in stress tolerance in response to environmental change.

Rapid local changes in stress tolerance can evolve in anthropogenically disturbed habitats (Reznik and Ghalambor 2001) and have potential ecological consequences for populations, communities, and ecosystems (Hairston et al. 2005). Studies in freshwater and marine systems detected heavy metal tolerance in invertebrates (Klerks and Weis 1987), resilience of corals to bleaching (Baker et al. 2004), altered behavior of copepods in response to low dissolved oxygen (Decker et al. 2003), and increased tolerance of zooplankton to cyanobacterial toxins following lake eutrophication (Hairston et al. 1999, 2001). Variation in acid tolerance has been detected among populations of frogs (Räsänen et al. 2003), fish (Rahel 1983), amphipods (France and Stokes 1987), and zooplankton (Price and Swift 1985; Fischer et al. 2001*b*). Individual populations often exist within a framework of complex community interactions. Few studies (but see Fischer et al. 2001*b*) have examined how historical exposure to an environmental stressor can influence community response to that stressor, particularly after it has been removed for several years.

In this study, we expand on the work of Fischer et al. (2001*b*) by investigating adaptive responses of crustacean zooplankton to large-scale regional acidification. We conducted a reciprocal transplant field enclosure experiment to test if the zooplankton community present in an acid-recovering boreal shield lake showed evidence of enhanced acid tolerance to historical acidification following 6 years of recovered (pH ≥ 6.0) lake-water pH. A secondary objective was to assess the influence of the local environment on survival and abundance of zooplankton that had been transferred from one lake to the other to determine if subtle differences in local water chemistry and food conditions between the buffered lake and the acid-recovering lake were limiting the recovery of species in acid-recovering lakes with pH ≥ 6.0.

Materials and methods

Our experiment was conducted in Killarney Provincial Park, Ontario, Canada, an area exposed to regional atmospheric acidification during the 20th century (Beamish and Harvey 1972; Sprules 1975). However, variation in local geology (Debicki 1982) resulted in lakes with different acidification histories (Dixit et al. 2002). We conducted our mesocosm experiments in two circumneutral lakes (pH ≥ 6.0) with different acidification histories: Carlyle and Ishmael lakes. We chose to use pH 6.0 as a threshold for circumneutral pH because it is a widely used measure for biological recovery of acid-sensitive species in the acidification recovery literature (Keller et al. 2002). Carlyle Lake, an acid-recovering lake, had a historical midsummer pH of 5.0 in 1972 (Sprules 1975), with pH values dipping as low as 4.5 during the spring of 1974 (Yan and Stokes 1978). By 1998, the lake had recovered to pH ≥ 6.0, a level that is commonly considered a threshold for biological recovery of acid-sensitive species (Keller et al. 2002). In contrast, Ishmael Lake is located in a watershed that contains outcrops of sandstone and limestone (Debicki 1982) and, as a result, has buffered lake water that never acidified below pH 6.0 (Dixit et al. 2002). Carlyle and Ishmael lakes were selected because they had similar physicochemical properties (Table 1) and zooplankton communities (Holt and Yan 2003) so that we could make community-level comparisons.

This 2 × 2 × 2 factorial design experiment (n = 3 replicates) was comprised of three main factors: incubation lake (IL; acid-recovering Carlyle Lake versus buffered Ishmael Lake), zooplankton source (ZS; Carlyle Lake zooplankton versus Ishmael Lake zooplankton), and pH (circumneutral pH ≥ 6.3 versus pH 4.8). With this experimental design, we were able to distinguish between effects caused by environmental variation between sites and differences among populations between study lakes. Twelve 3925 L polyethylene enclosures (1 m diameter × 5 m deep) were suspended from wooden frames in each of Carlyle and Ishmael lakes during the week of 25 June 2004. These enclosures extended through the epilimnion and were deep enough to have refuges for the zooplankton to avoid potential ultraviolet B (UVB) effects (1% UVB attenuation depth was approximately 3 m in both lakes).

The enclosures were filled with epilimnetic water from the lake in which they were anchored, which was filtered through 53 µm mesh to remove crustacean zooplankton but allow most algal species to pass through. After enclosures were filled with water, six enclosures in each lake were left at ambient pH (pH ~ 6.3 in Carlyle Lake and pH ~ 7.0 in Ishmael Lake) and the other six were acidified with 1 mol·L^{-1} sulfuric acid to pH 4.8.

During the next day, we reciprocally stocked zooplankton in the enclosures: half received zooplankton from the lakes in which the enclosures were suspended and the other half was stocked with zooplankton from the other lake. Zooplankton were collected by vertical tows with 35 cm diameter, 53 µm mesh nets and were stocked at ambient densities of the lake from which they came. There was no evidence of loss of certain taxa from getting caught on the surface film during the transfer process. Even if some zooplankton species had been preferentially lost over others, all animals were handled similarly and our comparisons were primarily done for populations within species and for aggregate community measures rather than between-species comparisons. Zooplankton for each treatment were collected by two teams, one at each lake. Half of the collected zooplankton was transported to the other lake, while the other half of the zooplankton remained in coolers at the side of the lake from which they were collected. All zooplankton were added to the enclosures at the same time, approximately 6 h after collection.

Zooplankton and water samples were collected from each enclosure once per week for 4 weeks. Week 0 samples were collected 1 to 2 days after zooplankton were added. Zooplankton were sampled by taking two vertical hauls from 5 m to the surface with a 15 cm diameter, 53 µm mesh net (4.5% of enclosure volume). Zooplankton from both hauls were pooled and preserved in a buffered 4% sugar–formalin solution for later enumeration. Water samples were collected

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Table 1. Selected physicochemical characteristics of study lakes included in the reciprocal transplant enclosure experiment.

Parameter	Carlyle Lake	Ishmael Lake
Latitude (N)	46°05′	46°06′
Longitude (W)	81°14′	81°35′
Watershed area (ha)	1058.6	1242.6
Lake area (ha)	156.7	72.8
Volume (m^3)	8 908 100	8 202 700
Maximum depth (m)	14.6	19.8
Total phosphorus ($\mu g \cdot L^{-1}$)	5.2	5.8
Dissolved organic carbon ($mg \cdot L^{-1}$)	4.1	4.1
Conductivity ($\mu S \cdot cm^{-1}$)	20.6	26.9
pH	6.3	7.0
pH in 1972 (Sprules 1975)	5.0 (pH < 6.0)	6.4 (pH > 6.0)
Acidification history	Acid-recovering	Buffered

Note: 2004 midsummer values are presented for total phosphorus, dissolved organic carbon, conductivity, and pH.

from 5 m to the surface in the enclosures with a weighted 2.5 cm inner diameter Tygon tube. These samples were stored in dark Nalgene bottles that were kept cool with ice packs in coolers until returning to the laboratory. pH and conductivity were measured in the laboratory using a WTW inoLab 740 pH/conductivity meter (WTW Inc., 6E Gill Street, Woburn, MA 01801, USA) on the day that samples were collected. To maintain the pH treatments, sulfuric acid was occasionally added to the enclosures on the following week if pH had drifted. An estimate of total chlorophyll *a* was obtained by collecting phytoplankton from a subsample of 80 µm filtered water on a Fisherbrand 1.2 µm pore size G4 glass fiber filter (Fisher Scientific Canada, 112 Colonnade Road, Nepean, ON K2E 7L6, Canada). A measure of edible chlorophyll *a* was obtained by filtering sample water through 30 µm mesh and then collecting the phytoplankton from the filtrate on a 1.2 µm pore size glass fiber filter as most zooplankton taxa graze most efficiently on highly edible, small algae (<30–35 µm) (Cyr 1998).

Crustacean zooplankton were enumerated with a protocol designed to target mature individuals that could be unambiguously identified to species, as well as to detect rare species (Girard and Reid 1990). Subsamples (10 mL) were taken from a standardized 50 mL sample volume, and at least 250 individuals were counted so that no more than 50 individuals for the dominant taxa, no more than 50 copepodids per order, and no more than 30 nauplii per order were included in the tally to 250 individuals, even though more may have been enumerated. Zooplankton were identified and counted using a Leica MZ16 dissecting microscope (Leica Microsystems (Canada) Inc., Suite 400, 111 Granton Drive, Richmond Hill, ON L4B 1L5, Canada). Taxonomic keys that were used included Hebert (1995) and Dodson and Frey (2001) for cladocerans, Smith and Fernando (1978) for copepods, Taylor et al. (2002) for Bosminidae, and Smith (2001) for general zooplankton identification. The taxa *Bosmina* spp. was identified only to subgenera because of taxonomic difficulties in distinguishing species. *Daphnia* species were pooled because of low abundances. Calanoid and cyclopoid nauplii were combined.

Statistical analyses

Shannon–Wiener indices, species richness, and total abundance were calculated for zooplankton on each sample day in each treatment (Magurran 2004). Shannon–Wiener indices of entropy were transformed to measures of diversity (Jost 2006). Because initial differences (week 0) were detected by factorial analyses of variance (ANOVAs) for all species abundances, community indices, and chlorophyll *a* concentrations, we used repeated-measures analyses of variance (RM-ANOVAs) to test for main effects (incubation lake, zooplankton source, and pH) on weeks 0 to 4. Individual species abundance data were $\log_{10}(x + 1)$ transformed and algal concentrations (total and edible chlorophyll *a*), species richness, and total abundance were $\log_{10}$ transformed to improve homogeneity of variances and normality. These results were presented despite the fact that most normality and equality of variance assumptions were violated because RM-ANOVA is robust to these violations when sample sizes are equal (Quinn and Keough 2002). Shannon–Wiener diversity and conductivity were not transformed because Levene's test and inspection of box plots indicated that ANOVA assumptions were met. Because we detected treatment differences on week 0, we considered time × treatment interactions using the Greenhouse–Geisser adjustment for departure from sphericity when necessary (Quinn and Keough 2002). RM-ANOVAs were followed by planned contrasts for significant time × treatment interactions to test for differences among sets of means that followed linear or quadratic trends (Quinn and Keough 2002). Sequential Bonferroni corrections were applied to sets of contrasts to control for family-wise error associated with multiple hypothesis testing. All RM-ANOVA, factorial ANOVA, trend analyses, and Bonferroni corrections were performed using Statistica 6.0 software (Statsoft Inc., 2300 East 14th Street, Tulsa, OK 74104). Post hoc power for RM-ANOVA with this experimental design was calculated with G-power software (Erdfelder et al. 1996).

To infer the influence of treatments on zooplankton community composition, we conducted principal components analysis (PCA) on species abundances that were averaged

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Table 2. Mean ± standard error of number of zooplankton per litre detected in week 0 among circumneutral treatments with "home" lake water: Ishmael zooplankton in circumneutral Ishmael Lake water and Carlyle zooplankton in circumneutral Carlyle Lake water.

	Ishmael Lake	Carlyle Lake
Acanthocyclops vernalis	Detected in week 1	Detected in week 1
Bosmina spp.*	1.91±0.48	0.72±0.58
Daphnia spp.	0.052±0.02	0.01±0.01
*Diacyclops bicuspidatus thomasi**	0.04±0.01	0.02±0.01
*Diaphanosoma birgei**	0.02±0.00	0.02±0.01
Epischura lacustris	0.02±0.01	0.02±0.00
*Holopedium gibberum**	0.14±0.03	0.64±0.14
*Leptodiaptomus minutus**	1.59±0.38	1.10±0.30
Leptodiaptomus sicilis	0.13±0.01	0.01±0.01
*Mesocyclops edax**	0.04±0.01	0.02±0.01
Sida crystallina	0.002±0.00	0
Skistodiaptomus oregonensis	0.18±0.03	0
Tropocyclops extensus	0.004±0.00	0.002±0.00
Calanoid copepodids	1.54±0.26	0.37±0.07
Cyclopoid copepodids	0.21±0.04	0.42±0.16
Nauplii	0.79±0.17	1.97±0.79

Note: Asterisks indicate taxa that were historically present in Carlyle Lake in 1972 during acidification (Spreules 1975).

over the last 3 weeks of the experiment (CANOCO 4.5 for Windows, with scaling that focuses on interspecies correlations; ter Braak and Šmilauer 1998). These averaged abundances were square root transformed to reduce the effect of high densities of a few taxa in the PCA. Although multivariate normality in the PCA could not be guaranteed, most species abundances followed univariate normal distributions. Factorial ANOVAs (Statistica 6.0) were performed on sample scores from the first and second PCA axes, respectively, to test for main and interaction treatment effects on the underlying community composition of zooplankton in the reciprocal transplant experiment. All assumptions of normality and equal variance were met for these factorial ANOVAs.

The results that we presented are focused on time interactions with main effects (incubation lake, zooplankton source, and pH) and on time interactions of zooplankton source with pH because we were primarily interested in testing if zooplankton response to pH was dependant on the acidification history of the source lake from which they were collected. This experiment also tested if there was an effect of incubation lake (local environmental factors) on zooplankton abundance and we therefore also considered time interactions with incubation lake × zooplankton source. Because our objective was to compare species found in both Carlyle and Ishmael lakes, we do not present RM-ANOVA results for species found only in one of these lakes nor do we present data for juvenile zooplankton unidentifiable to species (copepodids and nauplii) (Table 2).

Results

pH, conductivity, and algal concentrations

pH targets were achieved and maintained over the 4-week duration of the experiment. pH values (mean ± standard deviation) in circumneutral enclosures were 6.33 ± 0.12 in Carlyle Lake and 7.02 ± 0.13 in Ishmael Lake. Acidified enclosures in both lakes were pH 4.8 ± 0.15. Conductivity was slightly higher in Ishmael Lake than in Carlyle Lake (Table 1), and acid additions resulted in elevated conductivity in acidified treatments (33.4 ± 3.4 $\mu S \cdot cm^{-1}$ in Carlyle Lake and 39.3 ± 2.4 $\mu S \cdot cm^{-1}$ in Ishmael Lake) compared with circumneutral treatments (25.1 ± 4.4 $\mu S \cdot cm^{-1}$ in Carlyle Lake and 29.0 ± 1.3 $\mu S \cdot cm^{-1}$ in Ishmael Lake).

Chlorophyll *a* (chl *a*) concentrations were higher in enclosures with Carlyle Lake water than in mesocosms with Ishmael Lake water (comparison of linear trends for total chl *a*, Pillai's trace = 0.35, $F_{[1,16]} = 8.78$, $P < 0.01$; comparison of linear trends for edible chl *a*, Pillai's trace = 0.36, $F_{[1,16]} = 9.0$, $P < 0.01$) (Table 3; Fig. 1). Algal concentrations were dependant on the zooplankton population source (Table 3) because chl *a* concentrations were higher in enclosures containing zooplankton from Ishmael Lake than from Carlyle Lake (comparison of linear trends: total, Pillai's trace = 0.50, $F_{[1,16]} = 15.9$, $P < 0.01$; edible, Pillai's trace = 0.57, $F_{[1,16]} = 20.8$, $P < 0.01$; Fig. 1). We did not detect differences in linear trends that would indicate an overall acid effect on chl *a* concentrations throughout the experiment (Table 3; Fig. 1).

Community indices

There was a loss of species (comparison of linear trends, Pillai's trace = 0.67, $F_{[1,16]} = 32.9$, $P < 0.01$) in acidic enclosures, as indicated by a significant time × pH interaction (Table 3; Fig. 2). However, the response of species richness to pH treatment depended on the population source (Table 3, time × ZS × pH) as enclosures with Carlyle-source zooplankton maintained more species than enclosures with Ishmael-source zooplankton at acidic pH (comparison of linear trends, Pillai's trace = 0.47, $F_{[1,16]} = 14.3$, $P < 0.01$; Fig. 2). In addition, total abundance of zooplankton from Carlyle Lake was less impacted than zooplankton from Ishmael Lake in acidic enclosures (comparison of linear

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Table 3. Repeated-measures analysis of variance (RM-ANOVA) of time interactions for algal biomass (total chlorophyll *a* (Chl *a*), edible Chl *a*), zooplankton community responses (Shannon–Weiner diversity (S-W diversity), species richness, total abundance), and zooplankton population responses (*Bosmina* spp. (*Bos*), *Diacyclops bicuspidatus thomasi* (*D. bicus.*), *Diaphanosoma birgei* (*D. birg.*), *Holopedium gibberum* (*H. gibb.*), *Leptodiaptomus minutus* (*L. min.*), *Mesocyclops edax* (*M. edax*), *Epischura lacustris* (*E. lac.*), *Leptodiaptomus sicilis* (*L. sic.*), and *Tropocyclops extensus* (*T. ext.*)).

	Algal biomass		Community responses			Population responses								
	Total Chl *a*	Edible Chl *a*	S-W diversity	Species richness	Total abundance	*Bos.*	*D. bicus.*	*D. birg.*	*H. gibb.*	*L. min.*	*M. edax*	*E. lac.*	*L. sic.*	*T. ext.*
df effect	4	4	2.2	2.7	2.3	2.0	1.8	1.2	2.4	4.0	2.1	2.0	2.2	1.0
df error	64	64	35.3	43.7	36.7	31.3	29.3	19.6	39.2	64	32.9	31.3	35.4	16.0
Time × incubation lake (IL)														
F	10.00	10.00	6.70	2.88	11.41	9.78	6.20	—	3.67	3.14	—	—	5.59	8.13
P	**<0.01**	**<0.01**	**<0.01**	0.05	**<0.01**	**<0.01**	**<0.01**		**0.03**	**0.02**			**0.02**	**<0.01**
Time × zooplankton source (ZS)														
F	21.40	21.40	—	—	6.09	10.67	—	—	—	3.36	—	—	5.55	3.35
P	**<0.01**	**<0.01**			**<0.01**	**<0.01**				**0.01**			**0.02**	**0.02**
Time × pH														
F	19.70	19.70	—	10.44	3.93	7.47	—	4.10	7.03	2.96	35.77	4.28	—	4.87
P	**<0.01**	**<0.01**		**<0.01**	**0.02**	**<0.01**		0.05	**<0.01**	**0.03**	**<0.01**	**<0.01**		**<0.01**
Time × IL × ZS														
F	2.70	2.70	—	—	3.27	—	—	—	2.94	5.17	—	—	5.63	5.77
P	**0.04**	**0.04**			**0.04**				0.05	**<0.01**			**0.02**	**<0.01**
Time × IL × pH														
F	9.10	9.10	—	—	—	—	—	—	—	4.06	—	—	—	—
P	**<0.01**	**<0.01**								**<0.01**				
Time × ZS × pH														
F	9.70	9.70	—	3.02	6.27	—	—	—	7.85	—	3.37	—	—	—
P	**<0.01**	**<0.01**		**0.04**	**<0.01**				**<0.01**		0.05			
Time × IL × ZS × pH														
F	—	—	—	—	3.85	—	—	—	—	4.71	—	—	—	—
P					**0.03**					**<0.01**				

Note: *Acanthocyclops vernalis* and *Daphnia* spp. were not included in the table because no significant results were detected for these species. Bolded *P* values are significant at $P < 0.05$ and nonsignificant results are indicated by "—". *P* values and degrees of freedom (df) for time interactions were corrected with the Greenhouse-Geisser adjustment for any departures from sphericity.

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Fig. 1. Concentration ($\mu g \cdot L^{-1}$; mean ± standard error) of (*a*) total (<80 µm cell diameter) and (*b*) edible (<30 µm cell diameter) chlorophyll *a* in experimental enclosures in Carlyle and Ishmael lakes. Open symbols represent circumneutral enclosures; solid symbols represent acidified enclosures; triangles represent treatments with zooplankton from acid-recovering Carlyle Lake; circles represent treatments with zooplankton from buffered Ishmael Lake.

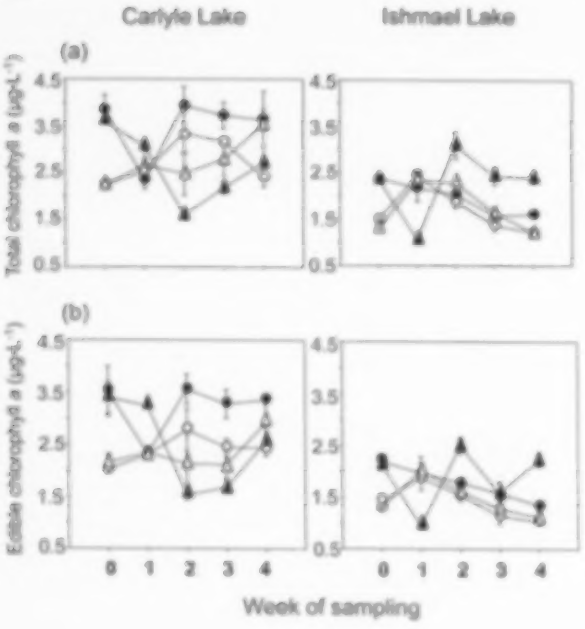
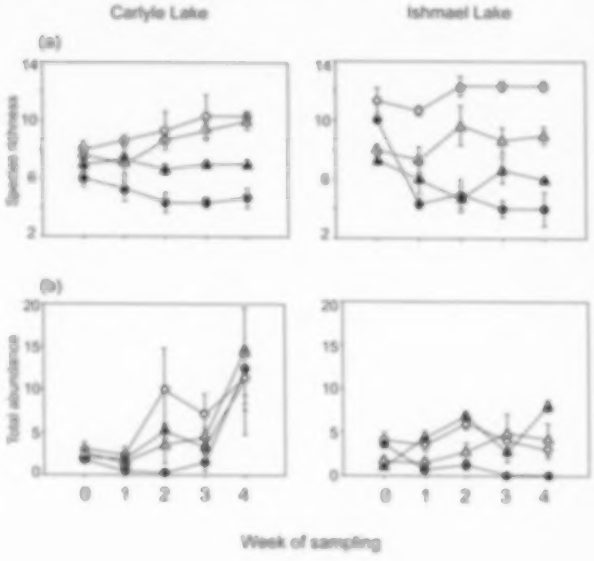


Fig. 2. Community indices of crustacean zooplankton (mean ± standard error) from enclosures in Carlyle and Ishmael lakes: (*a*) species richness and (*b*) total abundance. Open symbols represent circumneutral enclosures; solid symbols represent acidified enclosures; triangles represent treatments with zooplankton from acid-recovering Carlyle Lake; circles represent treatments with zooplankton from buffered Ishmael Lake.



trends, Pillai's trace = 0.55, $F_{[1,16]} = 19.3$, $P < 0.01$; Table 3; Fig. 2).

Species richness and total abundance were influenced by local environmental conditions (Table 3; Fig. 2). Species richness (comparison of linear trends, Pillai's trace = 0.30, $F_{[1,16]} = 6.86$, $P = 0.02$) was higher in enclosures with Ishmael Lake water compared with Carlyle Lake water. Although we found a significant time × incubation lake effect for Shannon–Wiener diversity (Table 3), slopes of linear trends between the two incubation lakes were not different. Total zooplankton abundance was greater in enclosures in Carlyle Lake than in Ishmael Lake (comparison of linear trends, Pillai's trace = 0.63, $F_{[1,16]} = 27.1$, $P < 0.01$; Table 3; Fig. 2). In enclosures with Ishmael Lake water, zooplankton from Carlyle Lake had higher total abundance than zooplankton from Ishmael Lake at acidic pH (comparison of linear trends, Pillai's trace = 0.64, $F_{[1,16]} = 28.7$, $P < 0.01$; Table 3; Fig. 2).

Community ordination

PCA indicated that ordination axes 1 and 2 explained 52.4% and 26.3% of variance in species data, respectively. A factorial ANOVA conducted on sample scores from the first PCA axis detected an overall influence of pH ($F = 24.29$, df = 1, $P < 0.01$) and a zooplankton source × pH interaction ($F = 5.63$, df = 1, $P = 0.03$) on zooplankton community composition. Zooplankton from historically acidified Carlyle Lake and buffered Ishmael Lake had opposite responses to acid treatment (Fig. 3*a*). For sample scores from PCA axis 2, we detected significant main effects of incubation lake ($F = 13.54$, df = 1, $P < 0.01$), zooplankton source ($F = 5.34$, df = 1, $P = 0.03$), and pH ($F = 14.67$, df = 1, $P < 0.01$). The response of the zooplankton community from Ishmael Lake depended on incubation lake on PCA axis 2 (Fig. 3*b*).

Individual species historically present during acidification

"Acid-tolerant" species present in Carlyle and Ishmael lakes in 1972 were *Bosmina* spp., *Daphnia* spp., *Diacyclops bicuspidatus thomasi*, *Diaphanosoma birgei*, *Holopedium gibberum*, *Leptodiaptomus minutus*, and *Mesocyclops edax* (Fig. 4; Sprules 1975). An effect of zooplankton source that was detected for *Bosmina* spp. (Table 3) in experimental enclosures was supported by differences in linear trends (Pillai's trace = 0.53, $F_{[1,16]} = 18.4$, $P < 0.01$) because more individuals came from Carlyle Lake than from Ishmael Lake across treatments. Zooplankton source was also significant for *L. minutus* (Table 3; Fig. 5), but we could not detect differences in linear patterns among treatments. The abundance of all species, except *D. bicuspidatus thomasi*, was significantly different in acid treatments compared with controls (Table 3; Fig. 5). Unlike *D. birgei* (comparison of linear trends, Pillai's trace = 0.21, $F_{[1,16]} = 4.29$, $P = 0.05$) and *M. edax* (comparison of linear trends, Pillai's trace = 0.85, $F_{[1,16]} = 87.5$, $P < 0.01$), the abundance of which decreased in acid treatments, *H. gibberum* flourished in acidic enclosures (comparison of quadratic trends, Pillai's trace = 0.52, $F_{[1,16]} = 17.2$, $P < 0.01$). Although we detected a significant

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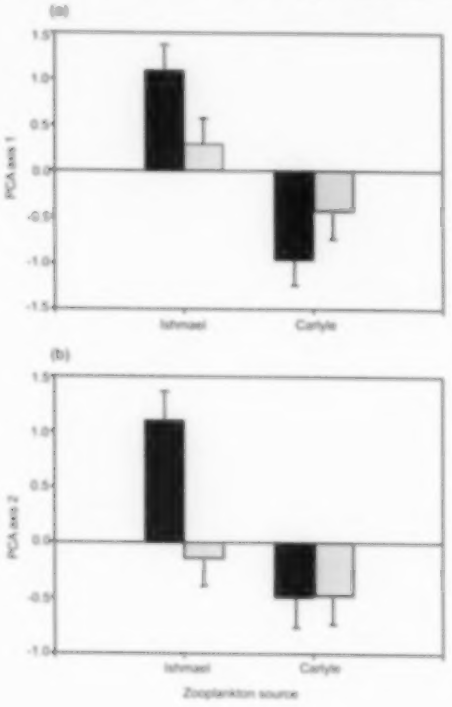
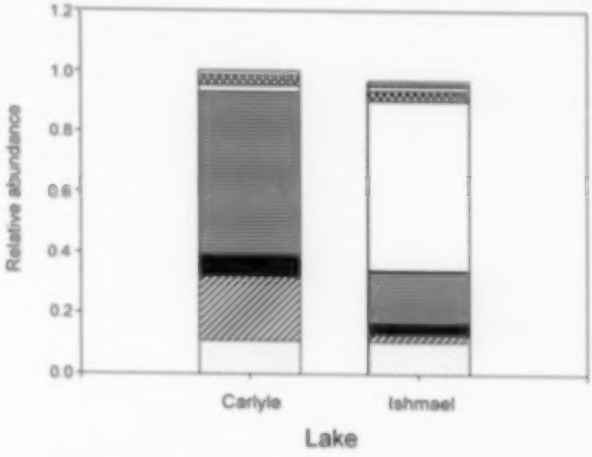
Fig. 3. Significant treatment interactions in zooplankton community composition detected from principal component analysis (PCA) sample scores: (*a*) a significant zooplankton source × pH interaction detected for axis 1 scores (solid bars indicate acidic pH; shaded bars indicate circumneutral pH) and (*b*) a significant zooplankton source × incubation lake interaction detected for axis 2 scores (solid bars indicate incubation in Ishmael lake water; shaded bars indicate incubation in Carlyle lake water).



pH × time effect for *Bosmina* spp. and *L. minutus*, we could not detect differences in linear trends among pH treatments.

The pH response depended on acidification history for *H. gibberum*, *L. minutus*, and *M. edax*, as indicated by significant zooplankton source × pH and incubation lake × zooplankton source × pH time interactions (Table 3). Acid tolerances of *H. gibberum* differed between lakes (Fig. 5) because more individuals from Carlyle Lake than Ishmael Lake were detected in acidic enclosures (comparison of quadratic trends, Pillai's trace = 0.57, $F_{[1,16]} = 21.0$, $P < 0.01$). The acid tolerance of *L. minutus* was dependant on zooplankton source (Table 3; Fig. 5). In this case, *L. minutus* from Carlyle Lake was more abundant than from Ishmael Lake when incubated in acidic enclosures with Carlyle lake water (comparison of linear trends, Pillai's trace = 0.32, $F_{[1,16]} = 8.0$, $P = 0.01$). *Leptodiaptomus minutus* individuals from Carlyle Lake also occurred in higher concentrations than individuals from Ishmael Lake when incubated in acidic enclosures with Ishmael Lake water (comparison of linear trends, Pillai's trace = 0.41, $F_{[1,16]} = 10.9$, $P < 0.01$). We detected a marginally significant time × zooplankton source × pH interaction for *M. edax* (Table 3) and could not detect significant differences in linear trends. *Mesocyclops edax* from both Carlyle (comparison of linear trends, Pillai's trace = 0.59, $F_{[1,16]} = 23.4$, $P < 0.01$) and Ishmael (comparison of linear trends, Pillai's trace = 0.81, $F_{[1,16]} = 70.4$, $P < 0.01$) lakes became more abundant in circumneutral enclosures than in acidic treatments (Fig. 5).

Fig. 4. Relative abundance of zooplankton (number of adults·L^{-1}) historically present in both acidic Carlyle and circumneutral Ishmael lakes in 1972 (Sprules 1975). From the bottom of the diagram to top: dotted bars, *Bosmina* spp.; diagonally striped bars, *D. birgei*; solid bars, *H. gibberum*; horizontally striped bars, *L. minutus*; open bars, *D. bicuspidatus thomasi*; checkered bars, *M. edax*; shaded bars: *Daphnia* spp.; gridded bar, *S. oregonensis* and *E. lacustris*, which were found only in Ishmael Lake in 1972.



With the exception of *D. birgei* and *M. edax*, species abundance was dependant on the lake in which a species was incubated (Table 3; Fig. 5). A greater concentration of *H. gibberum* was detected in enclosures in Ishmael Lake than in Carlyle Lake (comparison of quadratic trends, Pillai's trace = 0.21, $F_{[1,16]} = 4.29$, $P = 0.05$). Conversely, *D. bicuspidatus thomasi* (comparison of linear trends, Pillai's trace = 0.34, $F_{[1,16]} = 8.10$, $P = 0.01$) and *Bosmina* spp. (comparison of linear trends, Pillai's trace = 0.46, $F_{[1,16]} = 13.8$, $P < 0.01$) became more abundant in Carlyle Lake enclosures. For *L. minutus*, individuals from Carlyle Lake had greater abundance in Carlyle Lake than in Ishmael Lake (comparison of linear trends: Pillai's Trace = 0.26, $F_{[1,16]} = 5.72$, $P < 0.02$), and individuals from Ishmael Lake had greater abundance in Ishmael Lake than in Carlyle Lake (comparison of linear trends, Pillai's trace = 0.23, $F_{[1,16]} = 4.78$, $P < 0.03$; zooplankton source × incubation lake; Table 3; Fig. 5).

Individual species not historically present during acidification

Acid-sensitive species not historically present in Carlyle Lake or Ishmael Lake in 1972 were *Acanthocyclops vernalis*, *Leptodiaptomus sicilis*, and *Tropocyclops extensus*; *Epischura lacustris* was detected in Ishmael Lake (Sprules 1975). Ishmael Lake was a source of more *L. sicilis* individuals than Carlyle Lake (comparison of quadratic trends, Pillai's trace = 0.63, $F_{[1,16]} = 27.4$, $P < 0.01$; Table 3). *Epischura lacustris* (comparison of linear trends, Pillai's trace = 0.40, $F_{[1,16]} = 10.8$, $P < 0.01$) and *T. extensus* (com-

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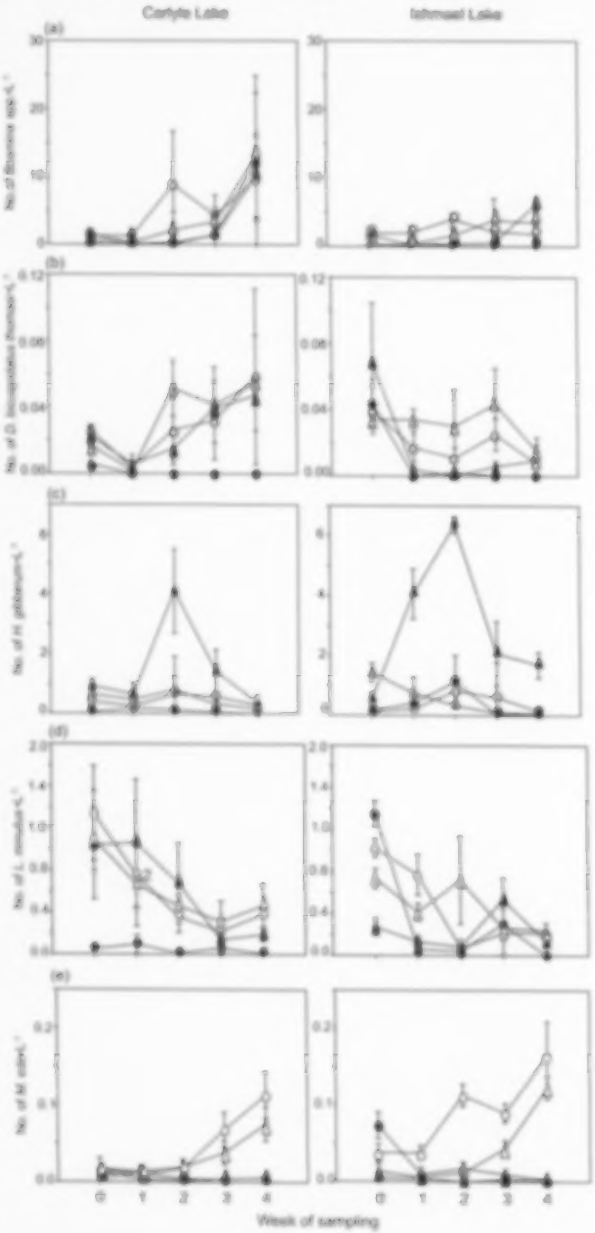
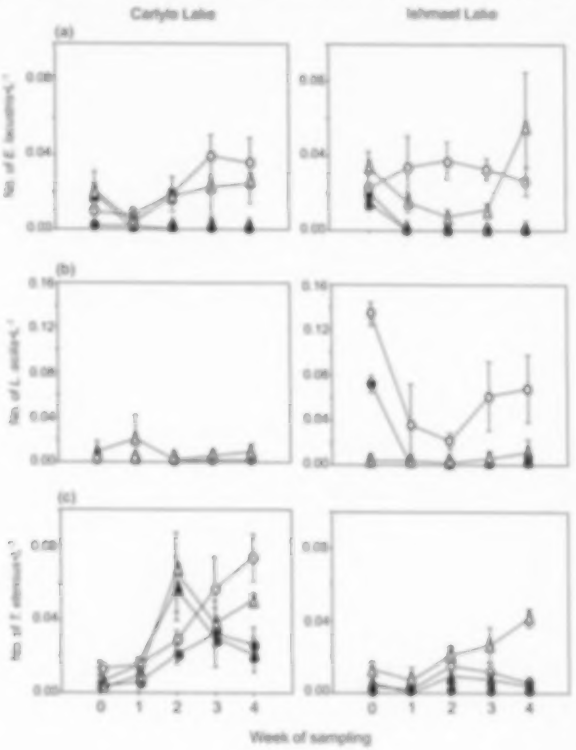
Fig. 5. Abundances in experimental enclosures of zooplankton taxa (number of adults·L^{-1}; mean ± standard error) that were historically present in both Carlyle and Ishmael lakes in 1972: open symbols, circumneutral enclosures; solid symbols, acidified enclosures; triangles, treatments with zooplankton from acid-recovering Carlyle Lake; circles, treatments with zooplankton from buffered Ishmael Lake. We did not detect any significant results for *Daphnia* sp. and only a marginal effect of pH on *Diaphanosoma birgei*, so these taxa were not included in the figure.



parison of linear trends, Pillai's trace = 0.48, $F_{[1,16]} = 14.8$, $P < 0.01$) were more abundant in circumneutral enclosures than in acidic enclosures (Table 3; Fig. 6). Not surprisingly,

Fig. 6. Abundances in experimental enclosures of zooplankton taxa that were not historically present in Carlyle Lake in 1972 (number of adults·L^{-1}; mean ± standard error): open symbols, circumneutral enclosures; solid symbols, acidified enclosures; triangles, treatments with zooplankton from acid-recovering Carlyle Lake; circles, treatments with zooplankton from buffered Ishmael Lake. We did not detect any significant results for *Acanthocyclops vernalis* and have not included this species in the figure.



these responses were not influenced by lake history as these taxa were historically absent in Carlyle during acidification and recolonized following lake-water recovery to pH ≥ 6.0. *Tropocyclops extensus* from Carlyle Lake incubated in acidic enclosures with "home" Carlyle Lake water increased until week 2 and then decreased. This treatment followed a similar time trend in circumneutral enclosures but increased again after week 3. Other treatment × time responses for this species were linear (Fig. 6).

Local environmental conditions influenced abundances of *L. sicilis* and *T. extensus* (Table 3). Although more *L. sicilis* individuals were detected in enclosures with Ishmael Lake water than Carlyle Lake water (comparison of quadratic trends, Pillai's trace = 0.67, $F_{[1,16]} = 32.1$, $P < 0.01$), there were more *T. extensus* individuals in enclosures with Carlyle Lake water than Ishmael Lake water (comparison of linear trends, Pillai's trace = 0.89, $F_{[1,16]} = 125$, $P < 0.01$; Fig. 6).

Discussion

We found differences in acid tolerances at the community level between lakes with different acidification histories. Al-

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though there was a reduction in species richness in acidified treatments in historically acidified Carlyle Lake, the reduction was not as great as in buffered Ishmael Lake. As a result, the zooplankton community from acid-recovering Carlyle Lake was more speciose than the community from buffered Ishmael Lake at acidic pH, and the converse pattern held at circumneutral pH. This response was primarily driven by acid-sensitive species in Ishmael Lake that were not detected in Carlyle Lake (*Skistodiaptomus oregonensis* and *Sida crystallina*). Total abundance was greatest in acidic enclosures in Ishmael Lake containing the zooplankton community with a history of acidification (Carlyle Lake), and this was likely driven by *H. gibberum*, which had peak abundances in acidified enclosures with Carlyle Lake as the zooplankton source. Therefore, local adaptation of key zooplankton species to past lake-water acidity may have driven community-level responses in Carlyle Lake for species richness and total abundance.

In our experiment, two key species, *H. gibberum* and *L. minutus*, contributed to community-level differences in acid tolerance of zooplankton with different lake acidification histories. Both species from Carlyle Lake appeared to be locally adapted to historical acidity, even though Carlyle Lake had a pH > 6 for 6 years. Fischer et al. (2001*b*) found a similar result for these taxa in Little Rock Lake, Wisconsin, after 2 years of recovery to pH 5.9. Acidic lakes with pH < 5.0 in the Killarney, Ontario, area frequently contain high abundances of *H. gibberum*, *L. minutus*, and *Bosmina* spp. (Sprules 1975; Holt and Yan 2003). Our data did not indicate any evidence for differences in acid tolerances among *Bosmina* spp. populations, which grew in abundance at both acidic and circumneutral pH regardless of population source. Other researchers have suggested that increases in *Bosmina* spp. following acidification occur because of indirect community effects caused by competitive release from larger cladoceran species that do not survive at acidic pH (Locke and Sprules 1993; Fischer et al. 2001*b*). It may be that *Bosmina* spp. can survive across a broad spectrum of pH but have an indirect response to acid. Acidification has been found to favour dominance by small zooplankton taxa, such as *Bosmina* spp. (Havens and Hanazato 1993).

We expected, but did not find, evidence of locally adapted acid tolerances in *D. bicuspidatus thomasi*, *D. birgei*, and *M. edax*. Acidic lakes with pH 5.0 to 5.2 often have zooplankton communities comprised of some combination of *D. biscuspidatus thomasi*, *D. birgei*, and *M. edax* in addition to other acid-tolerant species found in lakes with pH < 5.0 (Sprules 1975; Locke and Sprules 1993; Holt and Yan 2003). Past studies found evidence of increased acid tolerance in populations of *D. biscuspidatus thomasi* (Fischer et al. 2001*b*) and *M. edax* (Price and Swift 1985) from lakes with historic or current acidity. We found weak but statistically insignificant evidence for increased acid tolerance in *D. bicuspidatus thomasi* and no clear trends for *D. birgei* originating from Carlyle Lake. There are several hypotheses to explain why population-specific tolerance to acidity detected by Fischer et al. (2001*b*) in *D. bicuspidatus thomasi* and *M. edax* by Price and Swift (1985) was absent in our study: (*i*) geographical variation in population response; (*ii*) dispersal of acid-sensitive genotypes from other circumneutral lakes following pH recovery of Carlyle Lake; (*iii*) concentrations of individuals too low to detect differences; and (*iv*) loss of acid tolerance following lake recovery. Comparisons of the effects of experimental and atmospheric lake acidification in different regions have indicated similar declines in *D. bicuspidatus thomasis* and *M. edax* from lakes without a previous history of acidification (Schindler et al. 1991), and there is no evidence to suggest regional variation in population responses to pH for these species. Dispersal to Carlyle Lake from other circumneutral lakes is unlikely because, although the dispersal abilities of these cyclopoid copepods are unknown, many other copepod species are spatially dispersal-limited (Boileau and Hebert 1991; Zeller et al. 2006). *Diacyclops biscupidatus thomasi* concentrations were low and variable in our enclosures, and it is possible we did not have the statistical power to detect differences in acid tolerance among zooplankton sources. Our power to detect statistically significant differences at $\alpha = 0.05$ was low (critical $F_{[4,64]} = 2.52$, power = 0.592), even after assuming a relatively high effect size ($f^2 = 0.35$; Cohen 1988), reflecting trade-offs of logistics with conducting an experimental design with relatively low power. We suspect that differences in acid tolerance among *M. edax* populations from an acid pond and a circumneutral pond detected by Price and Swift (1985) could have been plastic responses adaptive in the maternal environment and lost within several generations under similar pH conditions. This is supported by results of Fischer et al. (2001*b*), who also failed to detect an adaptive response in *M. edax*. Loss of acid tolerance in years following recovery from acidification could be an explanation for the absence of adaptation to historical acidification in some species.

We did not measure the genetic component of acid tolerances in zooplankton but have circumstantial evidence to support genetically based local adaptation of acid tolerance in *H. gibberum* and *L. minutus*. Although both *H. gibberum* and *L. minutus* sexually produce resting eggs that accumulate in lake sediments with time, *Holopedium* spp. are cyclic parthenogens that alternate asexual reproduction with sex (Dodson and Frey 2001), and *L. minutus* is an obligately sexual species (Williamson and Reid 2001). Because most egg bank emergence occurs from the top 2 cm of lake sediment (Brendonck and De Meester 2003) and given that this depth interval involves the last 10 years of sedimentation in Killarney area lakes (Dixit et al. 1992), emergence from the egg bank into the water column would involve resting eggs produced when Carlyle Lake had recovered to around pH 6.0. Because at least several sexual generations of *H. gibberum* (one sexual generation in late summer per year) (Ward and Whipple 1959) and at least 50 to 75 generations of *L. minutus* likely occurred during that time, maternal effects from parents that directly experienced acidic conditions were likely minimized. Therefore, interpopulation differences in acid tolerance in *H. gibberum* and *L. minutus* were likely a result of local adaptation to historical lake-water pH.

Although there is evidence to suggest a genetic basis for adaptation to acidity in *H. gibberum* and *L. minutus*, this adaptation may be lost if it is associated with a fitness trade-off following lake-water recovery to pH 6.0. Our results showed that *L. minutus* was less strongly associated with acidic pH than *H. gibberum*. Other work found that *L. minutus* became locally adapted to historical acidification in many Killarney

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lakes but had a reduced acid tolerance after 6 to 8 years of recovered, circumneutral lake-water pH (Derry and Arnott 2007). This loss in acid tolerance with chemical lake recovery in *L. minutus* was associated with a physiological fitness trade-off (Derry and Arnott 2007). Adaptive reversals have also been found in other aquatic organisms, such as oligochaetes following the restoration of a metal-contaminated coastal marsh (Levinton et al. 2003). It is possible that *H. gibberum* maintained adaptation to historical pH in Caryle Lake because this cladoceran was not subject to the same physiological trade-off as *L. minutus* or because this species has undergone fewer generations following lake recovery. A similar experiment done in an experimentally acidified lake basin that recently recovered to pH 5.9 (<2 years; Fischer et al. 2001*b*) found four species with responses dependant on acidification history of zooplankton source (*H. gibberum*, *L. minutus*, *D. bicuspidatus thomasi*, and *T. extensus*). Only two of these species appeared to be locally adapted to historical acidification in Carlyle Lake, which had been circumneutral for a longer period of time (6 years). Because *T. extensus* was not detected during the period of acidification in Carlyle Lake, we did not expect to detect increased acid tolerance in this species. However, it is possible that we did not detect increased acid tolerance in some species because of adaptive reversals in acid tolerance that may have occurred in years following lake recovery from acidification.

Recovery of historically acidified Carlyle Lake resulted in colonization of acid-sensitive zooplankton that were not present when the lake was acidic (Sprules 1975) — the copepods *A. vernalis*, *E. lacustris*, *L. sicilis*, and *T. extensus*. Other research indicated that the abundance of these species is lower in acidic lake water (Keller and Pitblado 1984; Marmorek and Korman 1993). Although Fischer et al. (2001*b*) found evidence for increased acid tolerance in *T. extensus* populations following experimental acidification in Little Rock Lake, Wisconsin, this species appeared to be acid-sensitive in other regions (Schindler et al. 1991). The acid-sensitive copepods that we detected were either able to disperse into Carlyle Lake or were recruited from historic resting egg banks present in lake sediments (Williamson and Reid 2001) following lake-water recovery to pH 6.0. Because these copepods recently colonized the Carlyle Lake water column, it is not surprising that we did not detect local adaptation to low pH in these taxa.

Our experiment also tested if local environmental conditions affected zooplankton response when transplanted among lakes with similar physicochemical properties but different acidification histories. We examined this in two ways. (*i*) Did zooplankton, regardless of incubation lake, have higher abundances in either lake? (*ii*) Did zooplankton have higher growth and survival (and therefore higher abundance) in their "home" water compared with "transplant" water, particularly at circumneutral pH? We observed higher zooplankton abundance in Carlyle Lake likely because of higher algal concentrations. The establishment success of *D. bicuspidatus thomasi*, *Bosmina* spp., and *T. extensus* in Carlyle Lake enclosures compared with Ishmael Lake, despite the fact that more individuals were detected in Ishmael Lake than in Carlyle Lake enclosures during the initial week of the experiment, was probably related to the greater availability of food resources, as indicated by higher levels of chl *a* in Carlyle Lake. *Leptodiaptomus sicilis* was comparatively rare in the Carlyle Lake zooplankton community compared with the community from Ishmael Lake. This cyclopoid copepod established poorly in Carlyle Lake water compared with Ishmael Lake water and may be adapted to local water chemistry and (or) food resources in this lake. However, all other species, including those found only in the zooplankton community of Ishmael Lake (*S. oregonensis* and *S. crystallina*), were able to establish in enclosures with both home and transplant source water at circumneutral pH, suggesting that they were not specifically adapted to their similar home water conditions. In contrast, Forrest and Arnott (2006) found poor colonist establishment in an experiment in which zooplankton from nearby lakes were transplanted into enclosures in another Killarney lake. However, our enclosures did not contain the resident zooplankton community, whereas those of Forrest and Arnott (2006) did, suggesting that biotic interactions may be the primary determinant of colonist establishment in these circumneutral lakes. Further, high establishment of transplanted zooplankton in our experiment has important implications for the recovery of zooplankton communities because it suggests that local conditions in lakes of these types are suitable for most species and that other factors such as dispersal limitation and biotic interactions may be impeding recovery.

In conclusion, we found evidence for lasting effects of historical atmospheric acidification on the acid tolerances of some zooplankton taxa in a boreal shield lake after the passage of 6 years of recovered, circumneutral pH. Our findings support and extend the findings of Fischer et al. (2001*b*), who found similar responses for a zooplankton community after more recent recovery (<2 years) of a lake basin from experimental acidification. Adaptable acid tolerances in zooplankton communities may be important for maintaining certain ecosystem services, such as the maintenance of zooplankton biomass (Fischer et al. 2001*a*; Vinebrooke et al. 2003), in many lakes since the latest National Acid Rain Assessment (Meteorological Service of Canada 2004) reported that hundreds of thousands of lakes in eastern Canada will remain acidified at current levels of acid deposition. Of acidified lakes that do undergo chemical recovery, adaptation to past lake-water acidity may be advantageous when reacidification events occur from drought and climate change (Arnott et al. 2001). On the other hand, zooplankton with adaptable acid tolerances may have monopolized resources in acidified and acid-recovering lakes and may be contributing to the delayed recolonization of other acid-sensitive taxa as lakes recover from acidification (Yan et al. 2003; Binks et al. 2005; Frost et al. 2006).

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A state–space mixture approach for estimating catastrophic events in time series data

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Abstract: Catastrophic events are considered a major contributor to extinction threats, yet are rarely explicitly estimated in population models. We extend the basic state–space population dynamics model to include a mixture distribution for the process error. The mixture distribution consists of a "normal" component, representing regular process error variability, and a "catastrophic" component, representing rare events that negatively affect the population. Direct estimation of parameters is rarely possible using a single time series; however, estimation is possible when time series are combined in hierarchical models. We apply the catastrophic state–space model to simulated time series of abundance from simple, nonlinear population dynamics models. Applications of the model to these simulated time series indicate that population parameters (such as the carrying capacity or growth rate) and observation and process errors are estimated robustly when appropriate time series are available. Our simulations indicate that the power to detect a catastrophe is also a function of the strength of catastrophes and the magnitude of observation and process errors. To illustrate one potential application of this model, we apply the state–space catastrophic model to four west coast populations of northern fur seals (*Callorhinus ursinus*).

Résumé : Bien qu'on considère que les événements catastrophiques constituent des menaces d'extinction importantes, ceux-ci sont rarement estimés de façon explicite dans les modèles démographiques. Nous étendons un modèle démographique de base de type état–espace pour inclure une distribution de mélange de l'erreur de processus. La distribution de mélange comprend une composante « normale » qui représente la variabilité de l'erreur de processus ordinaire et une composante « catastrophique » qui représente les événements rares qui affectent la population de façon négative. Il est rarement possible d'estimer directement les variables à partir d'une seule série chronologique, mais cette estimation est possible lorsque plusieurs séries chronologiques sont combinées dans des modèles hiérarchiques. Nous utilisons le modèle état–espace catastrophique avec des séries chronologiques simulées d'abondance provenant de modèles de dynamique de population simples et non linéaires. L'application de ces modèles aux séries chronologiques simulées indique que les variables de la population (telles que le stock limite et le taux de croissance), ainsi que les erreurs d'observation et de processus, sont estimées avec robustesse lorsque des séries chronologiques appropriées sont disponibles. Nos simulations indiquent que la capacité de prédire une catastrophe est aussi fonction de la force des catastrophes et de l'importance des erreurs d'observation et de processus. Afin d'illustrer une application possible du modèle, nous utilisons le modèle état-espace catastrophique avec quatre populations d'otaries à fourrure du Nord (*Callorhinus ursinus)* de la Côte ouest.

[Traduit par la Rédaction]

Introduction

State–space population dynamics models have become increasingly popular in ecology with the advancement of new statistical methods and software capable of computing high-dimensional integrals. The main advantage of using state–space models is that both observation error and process error can be modeled simultaneously. Before the advent of these models, ecologists were forced to model only one of the two processes, assuming the other to be negligible. While this assumption may be valid for some populations, it is likely to introduce bias (Walters and Ludwig 1981). The most common application of state–space models has been to time series of population abundance data, because understanding natural fluctuations in population size is critical for management (de Valpine and Hastings 2002; Calder et al. 2003; Clark and Bjørnstad 2004). While a variety of processes may be responsible for observed fluctuations in abundance, the most important factors determining a species' persistence may be the frequency and magnitude of catastrophic events (Mangel and Tier 1994). Not including these events in stock assessments and population viability analyses (PVA) may create an overly optimistic view of a population's status (Young 1994).

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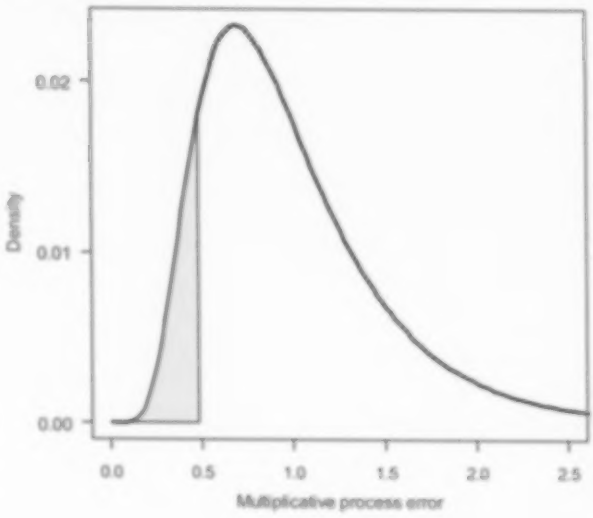
All natural populations are subject to a variety of stochastic processes, including both demographic and environmental variability (Lande et al. 2003). The key difference between these two types of stochasticity is that demographic variability is simply the random process of survival or reproduction, with each individual having the same probability of surviving or reproducing. Environmental variability changes the probability of survival or reproduction for every member of a population, but all individuals still experience the stochastic process of survival and reproduction. In this paper, we assume environmental stochasticity to be the dominant process. Most PVAs and stock assessments assume that the extreme events may be represented by the tail of the process error distribution (Hilborn and Mangel 1997; Fig. 1). The trade-off of using single distribution is that the frequency of extreme negative events can only be increased by increasing the variance, thereby also increasing the frequency of extreme positive events. For many *K*-selected species that experience slow growth, incorporating extreme positive growth events into population models is not biologically reasonable (e.g., even in the presence of unlimited resources, very few large-mammal populations would be able to experience an annual doubling in population size). As a more flexible approach, we adopt a mixture distribution to model environmental variation. This mixture consists of a distribution representing the normal process error variability of the population and a distribution representing the variability that the population experiences during catastrophes. Catastrophes have been given multiple definitions in the literature (Mangel and Tier 1994; Young 1994; Erb and Boyce 1999). We choose to adopt the definition that has been generally accepted in the ecological literature (Gerber and Hilborn 2001): a catastrophe represents a single, unpredictable, rare, negative event that affects the probability of survival or reproduction in a single time step and reduces a population by more than 50%. Some populations that have experienced steady declines over multiple years, such as the Western Aleutian stock of Steller sea lion (*Eumetopias jubatus*) (Angliss and Lodge 2002), would not be considered catastrophic under our definition.

A variety of approaches have been developed to address parameter estimation in a state–space framework. Numerical search algorithms such as the Kalman filter (Kalman 1960) are limited to linear problems with normal error distributions. More recently, restricted maximum-likelihood methods have been suggested (Staples et al. 2004), but these approaches also have some limitations. An extension of the Kalman approach, the numerically integrated state–space method, has been developed as a more general solution to both linear and nonlinear systems (de Valpine 2002; de Valpine and Hastings 2002). A third approach to state–space models are Bayesian statistics, which have seen increased use in fisheries science (Meyer and Millar 1999*b*; Rivot et al. 2004), and will be the focus of this paper. One advantage of dealing with state–space models in a Bayesian or numerically integrated state–space framework is that non-normal error distributions may be applied to nonlinear population models (Punt 2003). In a hierarchical modeling framework, Bayesian methods allow for multiple data sets to be combined in an analysis and for prior distributions to be placed on shared population parameters. While Bayesian methods may give similar results to traditional maximum likelihood approaches, the key difference is that Bayesian sampling integrates over the parameter space rather than maximizing (Hobbs and Hilborn 2006).

Fig. 1. Lognormal density with an expected value of 1.0 and coefficient of variation (CV) = 0.5. The region of the curve <0.5 has been shaded to illustrate those process errors that might be considered catastrophes (i.e., in this region, the population is reduced by more than 50%).



The objectives of this paper are to (*i*) develop a model for incorporating catastrophic events into time series of abundance data, (*ii*) evaluate the ability of Bayesian methods to estimate the underlying processes, (*iii*) evaluate the power of this method to detect catastrophic events, and (*iv*) apply the catastrophic model to west coast populations of northern fur seals (*Callorhinus ursinus*).

Materials and methods

The catastrophic state–space model

State–space models require the formulation of two models: an observation model and a process model describing the transition between unobserved population states. For time series of population abundance, the observation model relates the set of population abundance estimates based on observed data to the true unobserved states of the population. Typically, the observation model takes the form $\hat{N}_t = S_t\epsilon_t$, where $\hat{N}_t$ is the estimated abundance (e.g., from a survey), S_t represents the true unobserved abundance in year t, and ϵ_t is a multiplicative error term. The set of observation error terms, $\boldsymbol{\epsilon}$, are assumed independent between years and may be assigned any valid probability distribution (lognormal, gamma, etc.):

$$(1)\qquad P(\boldsymbol{\epsilon}_t \mid S_t, \sigma_\varepsilon) \sim \text{lognormal}\left(-\frac{\sigma_\varepsilon^2}{2}, \sigma_\varepsilon\right)$$

where S_t is the true population size.

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The general form of the state equation for the process component of the model is $S_{t+1} = g(S_t)\,\delta_t$, where the function $g(\cdot)$ represents a transitional relationship or growth function between states S_t and S_{t+1}, and δ_t is a multiplicative process error term. If a discrete theta-logistic growth model is used, for example (Gilpin and Ayala 1973), the process model can be written as

$$S_{t+1} = S_t\left[1 + r\left(1 - \frac{S_t}{K}\right)^{\theta}\right]\delta_t$$

where r is the logistic growth parameter, K is the logistic carrying capacity, θ controls the shape of density dependence, and the error term may again be assigned any distribution, e.g.

$$\delta_t \sim \text{lognormal}\left(-\frac{\sigma_p^2}{2}, \sigma_p\right)$$

Our catastrophic state–space model extends the basic state–space model by also assuming that each year of a particular time series is an unknown categorical state; it may be a normal year in which the population experiences regular process error variability, or it may be a catastrophic year in which the population experiences the variability associated with catastrophic events. There is no constraint placed on the magnitude of process errors in catastrophic years; the variability in those years may be less than or greater than the expected variability in normal years. Assuming independence between years, the chance of a catastrophe occurring in any particular year can be modeled as a Bernoulli trial with parameter ϕ, where ϕ represents the probability of a catastrophe (catastrophes representing successful trials). Using the laws of conditional probability, we can write this process as

$$P(S_{t+1}|Y_t, \boldsymbol{\beta}) = P(S_{t+1}|Y_t, \boldsymbol{\beta})\,P(Y_t|\phi)\,P(\phi)$$

where $\boldsymbol{\beta}$ represents a vector of all model parameters (population parameters, variances, etc.), and Y_t represents a categorical variable (normal or catastrophic year). The vector of categorical states may be treated as nuisance parameters, because they are integrated out of the model. The magnitude of a catastrophic event (θ) is modeled as a multiplicative term, so if the process errors are lognormally distributed, we have

$$\delta_t \sim \begin{cases} \text{lognormal}\left(-\frac{\tau_{norm}^2}{2}, \tau_{norm}\right) & \text{with } P(1-\phi) \\ \text{lognormal}\left(\theta - \frac{\tau_{cat}^2}{2}, \tau_{cat}\right) & \text{with } P(\phi) \end{cases}$$

The parameter controlling θ represents the average percent reduction in the population size; values close to 1.0 indicate that the population is nearly driven extinct. The probability density function of this mixture is described by the equation

$$(2)\quad P(\delta_t|S_{t-1}, \phi, \theta, \tau_{cat}, \tau_{norm}) = \frac{\phi}{\sqrt{2\pi}\,\tau_{cat}\,\delta_t}\exp\left\{-\frac{\left[\ln(\delta_t) - \theta + \frac{\tau_{cat}^2}{2}\right]^2}{2\tau_{cat}^2}\right\} + \frac{1.0-\phi}{\sqrt{2\pi}\,\tau_{norm}\,\delta_t}\exp\left\{-\frac{\left[\ln(\delta_t) + \frac{\tau_{norm}^2}{2}\right]^2}{2\tau_{norm}^2}\right\}$$

Priors and likelihood

A joint prior distribution must be assigned to all unobservable parameters and states in the model. There are two approaches to dealing with the prior distribution on the first state of the system: a prior may be placed on the state S_0, one time period before the first observation (yielding N conditional elements in the prior), or a prior may be placed on S_1, the state in the same time period as the first observation (yielding $N - 1$ conditional elements in the prior). In the catastrophic state–space model, we choose the latter approach, placing a prior on the first state, S_1. Assuming independence between parameters and conditional states, the joint prior for a simple logistic model can be expressed as follows:

$$(3)\quad P(r, K, \phi, \theta, \tau_{cat}, \tau_{norm}, S_1, S_2, \ldots, S_N) = P(r)P(K)P(\phi)P(\theta)P(\sigma_{ct})P(\tau_{cat})P(\tau_{norm})P(S_1)\prod_{t=2}^{N} P(\delta_t|S_{t-1}, r, K, \phi, \theta, \sigma_{ct}, \tau_{cat}, \tau_{norm})$$

If data on a particular species consisted of 10 observations over a 10-year period, there would be a total of 17 parameters (10 population states, 2 logistic parameters, 3 variance parameters, 2 catastrophe parameters). Choosing appropriate prior distributions must be done with caution, because arbitrary priors that are not informative with respect to one parameter may be informative with respect to another (Walters and Ludwig 1994; Punt and Hilborn 1997; McAllister and Kirkwood 1998). For the catastrophic parameters, we assigned a uniform (0, 0.5) prior to the probability of a catastrophe (ϕ) so that catastrophes would be constrained to be rare events. A uniform (0, 1) prior was placed on the magnitude of a catastrophe (θ) to express our vague knowledge about how much catastrophes reduce populations. Although this prior allows for events that are small in magnitude (e.g., a negative event might reduce a population by 3%), we do not consider values of $\theta < 0.5$ to represent catastrophes. For the purpose of this analysis, we assigned an uninformative uniform (0, 1) prior to the growth rate (r) and an informative lognormal prior to carrying capacity (K). Because we are assuming errors in the model to be lognormally distributed, the standard deviation of the error in log space can be interpreted as the coefficient of variation (CV) in normal space. We assumed that all three CVs were assigned inverse gamma prior distributions, because these priors are a common

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choice in Bayesian linear models (Gelman et al. 1995). The likelihood function of the data given the parameters is derived from eq. 1:

$$(4)\qquad L(r, K, \phi, \theta, \tau_{cat}, \tau_{norm}, S_1, S_2, \ldots | \hat{N}_2, \hat{N}_3, \ldots) = \prod_{i=1}^{N} P(\epsilon_i | S_i) = \left(\frac{1}{\sqrt{2\pi}\,\sigma_o}\right)^N \exp\left[-\frac{1}{2\sigma_o^2}\sum_{i=1}^{N}(\epsilon_i - 1.0)^2\right]$$

or distribution (eq. 3) and the likelihood (eq. 4).

Several methods are available to generate samples from the posterior. Thomas et al. (2005) implemented a sequential-importance-sampling (SIS) approach, which appears to give similar results to Markov chain Monte Carlo (MCMC) based approaches. Metropolis sampling methods have also been applied to state–space models; however, the most popular methods have been Gibbs sampling (or adaptive rejection sampling) implemented in WinBUGS (Meyer and Millar 1999*a*; Spiegelhalter et al. 2003). We chose to implement the catastrophic state–space model in WinBUGS because the batch-mode feature of WinBUGS 1.4 enabled us to do large-scale simulations on many machines.

Simulations

Relative to population models that only consider observation error or process error, state–space models are generally data-hungry. Adding a mixture distribution to the basic state–space model introduces a further layer of complexity. When the catastrophic state–space model is fit to a single time series of data, one of the two process error variances generally converges to zero, because the model is unable to separate the components of the mixture. An alternative approach is to combine multiple time series from multiple populations. In a hierarchical setting, this would allow each population to have unique population parameters (e.g., growth rates, carrying capacities), with the only assumption being that process error variances are shared between time series. A further layer of complexity may be to combine time series from multiple species in multiple environments, each with different probabilities of catastrophes.

We generated 10 000 random data sets to test the catastrophic state–space model, where each data set represented a collection of two–five time series, representing data from similar species in the same environment. We assumed that these populations experienced the same observation and process errors and were affected by catastrophes similarly (e.g., the probability and magnitude of a catastrophe is assumed constant across time series in a data set). Each of the time series within a data set consisted of 5–25 simulated observations. We chose to initially consider only the exponential growth and theta-logistic models as simulation models, but each time series was allowed to have unique population parameters (initial population sizes, growth rates, carrying capacities). Observation error and process error were assumed to be lognormally distributed. The probability and magnitude of catastrophes was independent between years and time series (ϕ ranged from 0.01 to 0.2, θ ranged from 0.6 to 0.9). Instead of drawing random values of the observation and process error standard deviations for each data set, we considered each of the standard deviations to be random factors (each ranging from 0.0 to 0.6 in steps of 0.05). For some of the time series, we generated large negative process error events in the absence of catastrophes to evaluate the ability of the model to distinguish between these two types of decline. Although they are unlikely to occur, these large negative events represent the tail area of a single process error distribution (Fig. 1).

To monitor MCMC convergence, we implemented the CODA package in R (www.r-project.org). In addition to monitoring the trace plots, autocorrelation plots, and densities of each parameter, the Geweke and Heidelberger–Welch statistic were used to determine whether or not chains had converged (Gelman et al. 1995; Gilks et al. 1996; Carlin and Louis 2000). Following a burn-in of 20 000 elements, we conducted 30 000 sampling iterations, saving every 10th draw to create a posterior sample of 3000 elements of each parameter per data set. After parameters for each simulated data set were estimated, the bias was calculated for each parameter as $\hat{\theta} - \theta$ (the true value of the parameter subtracted from the parameter estimate from the posterior distribution).

Application: northern fur seals

To illustrate one potential application of our state–space catastrophe model, we considered the west coast population of the northern fur seal. Previous analyses have estimated the total probability of catastrophes in the otariid family to be in the range of 0.25–2.1%·year^{-1} (Gerber and Hilborn 2001). Historically, pup counts have been used as indices of abundance for many otariid species (e.g., Loughlin et al. 1994). The number of pups in a given year may be estimated with precision, because pups usually remain on land, concentrated in small spatial locations. Northern fur seal pup abundance data has been collected by the National Marine Fisheries Service (NMFS) at four rookeries: the Pribilof Islands (St. George, St. Paul), Bogoslof Island, and San Miguel Island. Surveys on the Pribilof Islands have been conducted since the 1950s, while counts on Bogoslof and San Miguel have been initiated more recently (1980 and 1968, respectively, when the rookeries were discovered). The *C. ursinus* populations that breed on the Pribilof Islands constitute approximately 90% of the US population and 60% of the global population (York et al. 2000). The remaining 40% of the global population is found in the western Pacific (Kuril Islands, Tyuleniy Island, Commander Islands); however, annual surveys do not exist for these populations. Data from NMFS surveys since 1960 (annual counts 1960–1990, biennial counts after 1990) indicate that pup production on the St. Paul and St. George rookeries has been declining (Towell et al. 2006; Fig. 2), and the cause for the decline remains unknown. Many of the Pribilof pup estimates have associated standard error estimates, which are computed based on the traditional Lincoln–Peterson mark–recapture estimator (Seber 1982). The CVs based on these standard er-

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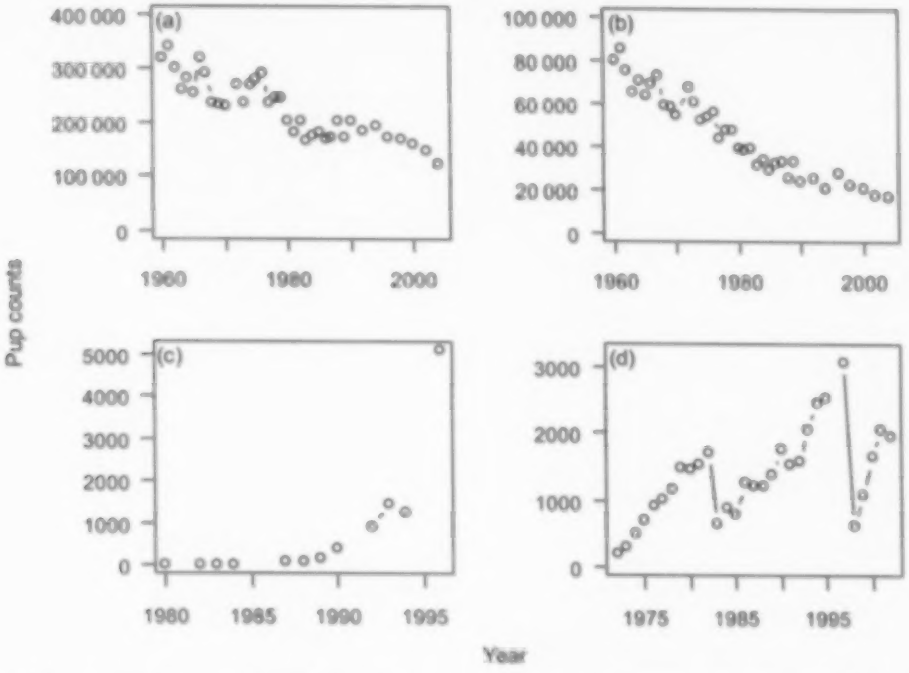
Fig. 2. Estimates of northern fur seal (*Callorhinus ursinus*) pup abundance for four US populations. The Pribilof Islands — (*a*) St. Paul, (*b*) St. George — and (*c*) Bogoslof Island are located in the Bering Sea, while (*d*) San Miguel Island is located off the coast of southern California.



rors are generally quite small because of large sample sizes (CVs < 0.10) and may underestimate the true measurement error of the NMFS surveys. Surveys of *C. ursinus* pups on Bogoslof Island were initiated by NMFS when the rookery was established in 1980, and although the surveys have not been conducted annually, the observations appear to show an increasing exponential trend in production (Fig. 2). Production for the San Miguel stock also has shown an increasing trend, but has experienced several catastrophic events. These negative events may be partially caused by El Niño (York 1991), but the effects are not completely understood. While the two largest declines in San Miguel pup production occurred during strong El Niño years, the *C. ursinus* population on San Miguel has experienced several other El Niño years (such as the ones that occurred over the period 1990–1994), with no apparent decline in pup numbers. While interannual fluctuations in the number of births is expected, pup production of both stocks may also be impacted by occasional catastrophic events. Catastrophic reductions in the number of *C. ursinus* pups may be an indicator that pup survival is impacted by catastrophes, but may also be an indicator of changes in the population dynamics of mature adults. If a catastrophe such as a disease outbreak were to reduce, for instance, adult survival (fewer adults results in less production) or adult fecundity, the catastrophe would be reflected by a drop in the number of births.

In developing a group of candidate models for this analysis, we extended the models used for the simulated time series by considering both population-specific parameters and ecosystem-specific parameters. Each of the four rookeries was allowed to have an island-specific growth equation. Pup counts at Bogoslof and San Miguel appeared to be increasing exponentially and were represented by the two-parameter model: $S_{t,j} = S_{0j} \exp(tr_j)$, where r_j is the rate of change for population j. Counts at St. George and St. Paul appeared to show the opposite trend (Fig. 2). Two alternative models were considered for the St. George and St. Paul rookeries: a two-parameter exponential model (similar to the one used for Bogoslof and San Miguel) and a three-parameter exponential decay model that was used in previous population assessments (York et al. 2002). This latter equation can be represented as $S_{t,j} = a_j + b_j 2^{(1960-t)/c_j}$, where a_j is a parameter representing equilibrium pup level (asymptote) for population j, b_j is a parameter representing the total decrease in annual pup production between 1960 and the equilibrium level a_j, and c_j is a decay term representing the half-life for population j. Growth rates in the models (r, b) were assigned uniform prior distributions, while the equilibrium (a) and decay term (c) were assigned gamma prior distributions. The equilibrium parameter represents the asymptotic production for each population, and the decay parameter represents the time necessary for the number of pups to decrease to half the difference between the number of pups at time zero and the asymptotic number of pups.

We assumed that the two catastrophe parameters in the model were ecosystem-specific, so that ϕ_j and θ_j represented the probability and magnitude, respectively, of catastrophes affecting the jth population. The primary justification in not allowing the catastrophe parameters to be shared across all populations is that the San Miguel Island population experiences El Niño events, while the Bering Sea populations do not. We were forced to assume that the process

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Table 1. Deviance information criterion (DIC) values for a set of 48 candidate models describing trends in northern fur seal (*Callorhinus ursinus*) pup production.

St. Paul parameters	St. George parameters	Catastrophe	Extra CV	1 CV	2 CVs	3 CVs
3	3	Y	Y	114.9	67.5	50.1
3	3	N	Y	164.6	102.6	107.0
3	**3**	**Y**	**N**	**48.8**	**15.6**	**0.0**
3	3	N	N	104.6	52.4	52.8
2	2	Y	Y	102.7	93.7	84.8
2	2	N	Y	171.3	134.4	135.0
2	2	Y	N	50.4	27.7	12.4
2	2	N	N	109.5	66.4	66.9
2	3	Y	Y	94.4	68.2	51.1
2	3	N	Y	143.2	108.4	111.4
2	3	Y	N	48.9	20.2	5.0
2	3	N	N	108.1	57.7	70.5
3	2	Y	Y	113.3	70.2	63.6
3	2	N	Y	165.1	122.7	123.2
3	2	Y	N	45.3	20.9	17.5
3	2	N	N	106.7	63.4	60.1

Note: Models may be represented as basic state–state models or as state–space mixture models (including catastrophes) and may contain additional observation error in the form of an additive coefficient of variation (CV) parameter. For each model, the state transition equations on Bogoslof Island and San Miguel Island are assumed to be two-parameter exponential models. Pribilof populations (St. Paul, St. George) may be modeled as two-parameter or three-parameter exponential decay models. Scenarios with 1 CV constrain the observation error CVs for all surveys in years without standard error estimates to be constant across the four populations; scenarios with 2 CVs allow the Pribilof surveys to have separate observation error CVs from the Bogoslof and San Miguel surveys; and scenarios with 3 CVs allow Bogoslof and San Miguel to have island-specific observation error CVs (the Pribilof populations are assumed to share the same CV). The best-fit model with the lowest DIC score is highlighted in bold.

error variances (not the process errors themselves) were shared across all four populations, because the San Miguel time series alone would not be able to separate the components of the process error mixture for a model that allows ecosystem-specific variances. For each ecosystem, we assigned uniform (0, 0.5) priors to ϕ_i and a uniform (0, 1) prior to θ. This latter prior was chosen to include all negative events; however, only those in the range 0.5–1.0 will be interpreted as catastrophes.

As an extension of the catastrophe model previously applied to simulated data, we assumed that observation error and process errors in all candidate models were multiplicative gamma distributions. There are several possible parameterizations of the gamma distribution; however, we chose to adopt a two-parameter version dependent on a shape parameter and CV parameter. To evaluate whether there was evidence for the catastrophic state–space model over the standard state–space model, we considered some models with a single process error distribution. All process error CVs were assigned gamma prior distributions with an expected value of 0.2.

To assess whether a model that incorporated additional observation uncertainty was appropriate, we developed several models that included additional observation error parameters. Because not all years had standard error estimates present, we were forced to assume that the CV for years with missing estimates was constant (CV_c). In the first set of models (1 CV, Table 1), we assumed that the CV for the ith year and jth population could be modeled as $CV_{i,j} = \sqrt{CV_{est(i,j)}^2 + CV_{extra}^2}$ if the standard error estimate did exist ($CV_{est(i,j)}$ being the CV calculated from the abundance and standard error estimates) and $CV_{i,j} = \sqrt{CV_c^2 + CV_{extra}^2}$ otherwise. One problem with assuming that the CV is constant when standard errors don't exist is that surveys conducted on the Pribilof Islands may have a different CV than surveys conducted on Bogoslof Island or San Miguel Island. The justification for this difference is that pup estimates from the Pribilofs represent mark–recapture estimates, while Bogoslof and San Miguel counts are direct counts based on single observations. To account for this additional variation, we developed a second set of models (2 CVs, Table 1) that allowed the observation error CV for Bogoslof and San Miguel to differ from that of the Pribilof surveys (but which was assumed constant between years and between the two islands). Finally, we developed a third set of models (3 CVs, Table 1) that allowed the Bogoslof and San Miguel populations to have unique, island-specific observation error CVs. All observation error CVs were assigned gamma prior distributions with a mean of 0.2, with the exception of the additive parameter (CV_{extra}), which was assigned a uniform prior distribution.

All combinations of population models, process errors, and observation error scenarios yielded a total of 48 candidate models. MCMC parameter estimation for each model was done via MCMC in WinBUGS 1.4. After a burn-in of 2.0×10^5 iterations, we thinned the next 5.0×10^5 elements of the MCMC chain, retaining every 100th sample. The deviance information criterion (DIC) was also computed as a model selection tool (Spiegelhalter et al. 2003). In some instances, DIC may behave similarly to the widely used

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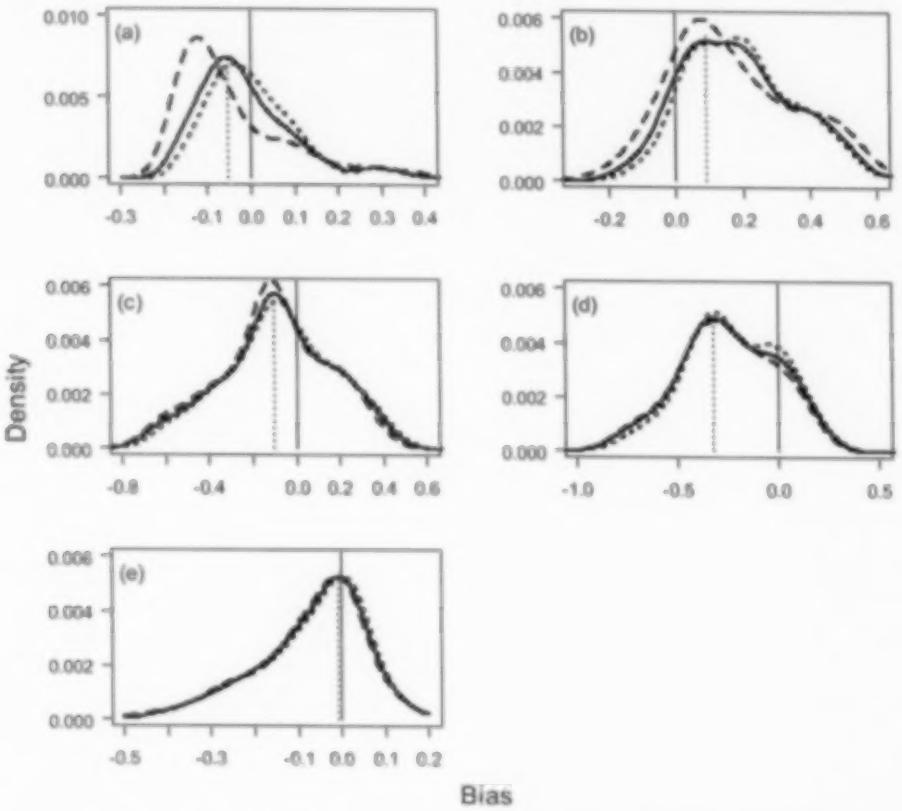
Fig. 3. Density plots of the bias in posterior estimates of the probability of a catastrophe (ϕ, panel *a*), the magnitude of a catastrophe (θ, panel *b*), the observation error coefficient of variation (CV) (σ_v, panel *c*), process error CV in normal years (τ_{norm}, panel *d*), and process error CV in catastrophic years (τ_{cat}, panel *e*). The solid line represents the distribution of the median bias (posterior median minus true value), the short broken line represents the bias of the posterior mode, and the longer broken line represents the bias of the posterior mean.



Akaike's information criterion (AIC, Akaike 1973), with the major difference being that DIC integrates over the parameter space (instead of maximizing). The DIC computation can be expressed as $DIC = D(\hat{\theta}) + 2p_D$, where $D(\hat{\theta})$ represents the deviance evaluated at the posterior mean, and p_D represents the effective number of model parameters. The term p_D can also be expressed as the deviance function evaluated at the expected posterior values of the parameters subtracted from the mean deviance across all parameter vectors, $p_D = \overline{D(\theta)} - D(\hat{\theta})$.

Results

Of all parameters in the catastrophic state–space model, we found the population parameters to be estimated robustly, but parameter estimates were sensitive to the initial state in the simulation model. This result is expected, as the same result holds under simpler error models (e.g., models that consider observation or process error only). For the case where the simulation model is logistic, a time series with low relative population size provides information about the initial state and population growth rate, but little or no information about carrying capacity. The opposite is also true — when the initial population state is close to carrying capacity, estimates of the initial state and growth rate are biased; however, estimates of K are relatively unbiased. Bias in estimating ϕ was slightly negative, indicating that the parameter was underestimated more frequently than it was overestimated (Fig. 3). The opposite result was true for estimating θ — the bias tended to be positive, indicating that the parameter tended to be overestimated. Bias in the observation error is centered close to zero, indicating that this parameter and process error in normal years is centered close to zero; however, bias in estimating the process error in catastrophic years appears to be positive (Fig. 3).

One necessary feature of the catastrophic state–space model is that it must be able to distinguish catastrophes from anomalies caused by negative process errors. Because we know each catastrophe in the simulated time series, it is possible to quantify both the ability of the model to detect catastrophes and the error rate with which the model classifies normal variation as catastrophes. Statistical power has been applied to many situations in biology (Taylor and Gerrodette 1993), and for the purpose of this analysis we define power as the ability to detect a catastrophe when it actually occurs. The parameters that affect the power to detect catastrophes

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Fig. 4. The relationship between the power to detect a trend (solid circles) and percent reduction in population size (i.e., the magnitude of a catastrophe). Also included is the probability of falsely detecting a catastrophe (open circles). Power is calculated across all levels of observation error and process errors.

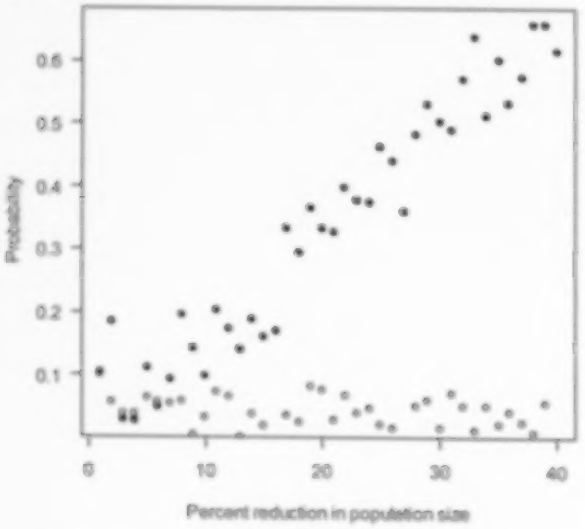
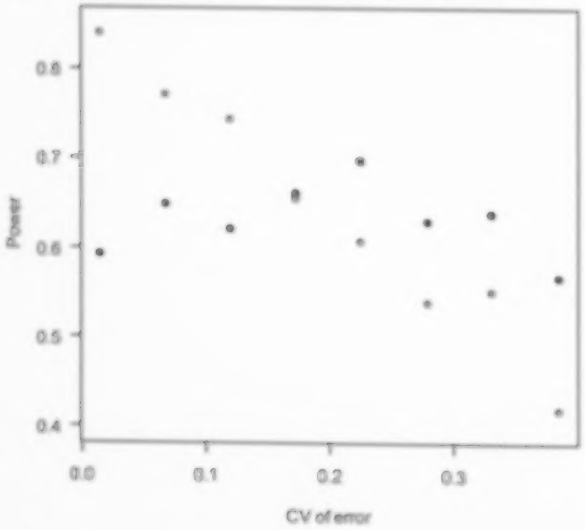
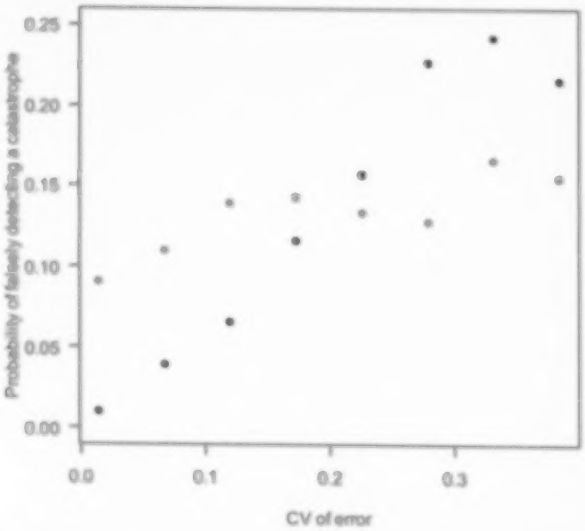


Fig. 5. The relationship between the coefficient of variation (CV) of the errors (when the errors are lognormally distributed) and the power to detect a catastrophe for 1000 data sets. The magnitude of a catastrophe is held constant at 0.6 across all data sets. Open circles represent varying levels of observation error (across all levels of process error), and solid circles represent varying levels of process error (across all levels of observation error).



in our state–space model are θ and the magnitude of the observation and process errors. As catastrophes become more severe, the probability of detecting them increases (Fig. 4). Observation error appears to have a larger effect on power than process error (Fig. 5); however, both influence the rate

Fig. 6. The relationship between the coefficient of variation (CV) of the errors (when the errors are lognormally distributed) and the probability of falsely detecting a catastrophe for 1000 data sets. The magnitude of a catastrophe is held constant at 0.6 across all data sets. Open circles represent varying levels of observation error (across all levels of process error), and solid circles represent varying levels of process error (across all levels of observation error).



of falsely detecting a catastrophe (Fig. 6). At intermediate values of the observation error (CV > 0.35), the probability of detecting a catastrophe that reduces the population by 60% becomes less than would be expected by chance alone. As expected, the power to detect catastrophes is highest under low levels of observation and process error and when catastrophes are large in magnitude.

Of the remaining 48 candidate models, the model with the lowest DIC score appeared to be a model that included catastrophes, allowed both Pribilof populations to follow three-parameter exponential curves, and allowed both Bogoslof Island and San Miguel Island to have unique island-specific observation errors (Table 1). This model was strongly favored over the alternative models, receiving 97.5% of the normalized DIC weight. One of the most important results from the model selection procedure was that the state–space model that incorporated catastrophes was always favored over the simpler model with a single process error distribution. This result is important because it indicates that catastrophes should be included in our analysis, regardless of which population models are chosen. A second important result is that for nearly all scenarios, there appears to be no evidence for the inclusion of an additional observation error parameter, suggesting that the estimated CVs for the Pribilof surveys are appropriate.

For the model with the lowest DIC score, the posterior mode of ϕ was found to be 0.019 for Bering Sea populations (2.5% = 0.001, 97.5% = 0.462) and 0.072 for the San Miguel population (2.5% = 0.021, 97.5% = 0.228; Fig. 7). The posterior mode of θ for the San Miguel population was estimated to be 0.751 (2.5% = 0.591, 97.5% = 0.801). The

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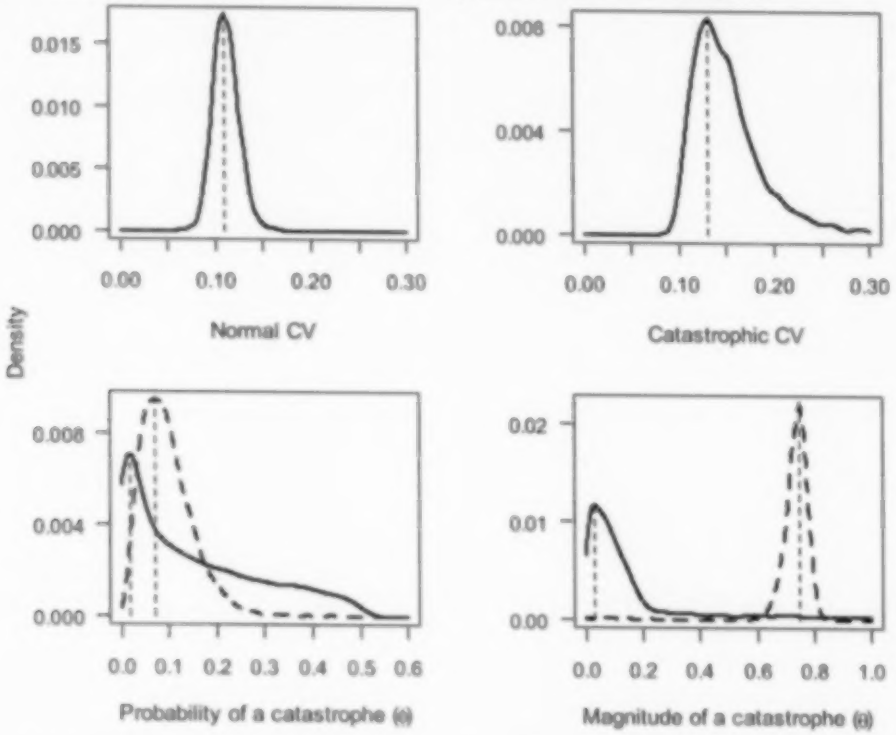
Fig. 7. Posterior probability distributions for the process error parameters and catastrophe parameters for the model with the lowest deviance information criterion (DIC) score. Posteriors of the process error coefficients of variation (CVs) indicate that the variation in catastrophic years (catastrophic CV) is more skewed than the normal variability (normal CV). Because we allow the probability of a catastrophe and magnitude of a catastrophe to vary by ecosystem, two posterior distributions are presented (solid line, Bering Sea; broken line, San Miguel Island). The broken vertical line represents the posterior mode of each distribution.



value of θ in the Bering Sea was estimated to be close to zero, indicating that while the Bering Sea populations might experience chance reductions in the number of pups, the populations do not experience true catastrophes. There are several important differences between the estimated process error CVs in normal and catastrophic years (Fig. 8). First, the posterior mode of the CV in catastrophic years (0.129) is larger than the mode of the CV in normal years (0.109), implying that there is slightly more process uncertainty in catastrophic years. The variance of the estimated process error CV in catastrophic years is greater than that in normal years. For example, approximately 17% of the estimated process error CV in catastrophic years is greater than the upper bound of the process error CV in normal years (~0.16). This result is somewhat intuitive. Because the number of catastrophic years is relatively small compared with the number of normal years, the process error variation in catastrophic years is expected to be estimated with less precision.

Discussion

The catastrophic state–space model could be applied to a wide range of species, including both terrestrial and marine organisms. One potential source for combining continuous time series in a meta-analysis is the Global Population Dynamics Database (NERC 1999), which has collected over 5000 time series from the ecological and fisheries literature. Applications of the catastrophic state–space model should not be limited to parameter estimation or hypothesis testing — incorporating a more realistic form of catastrophic events will have dramatic implications for population projections and management decisions. The most useful case of the model is the scenario where lengthy time series from similar populations (or even metapopulations) are combined in a hierarchical model.

The data sets in our simulations included a range of realistic observation and process errors, with CVs ranging from 0.01 to 0.5. Across all simulations, the population parameters (e.g., logistic parameters), observation error, and process error in normal years were estimated robustly. The ability of the model to estimate the catastrophic parameters (ϕ, θ, τ_{cat}) was highly dependent on the frequency and magnitude of catastrophes involved. The relationship between the magnitude of the catastrophic parameters and the bias in estimating them is somewhat intuitive — as catastrophes become more frequent and stronger, the model is better able to discriminate them from normal years with extreme process error, thereby decreasing the bias.

One potential criticism of this model is that for some data sets (particularly those in which no real catastrophes exist), the magnitude of a catastrophe may be estimated as being approximately 1.0 and the probability of a catastrophe may

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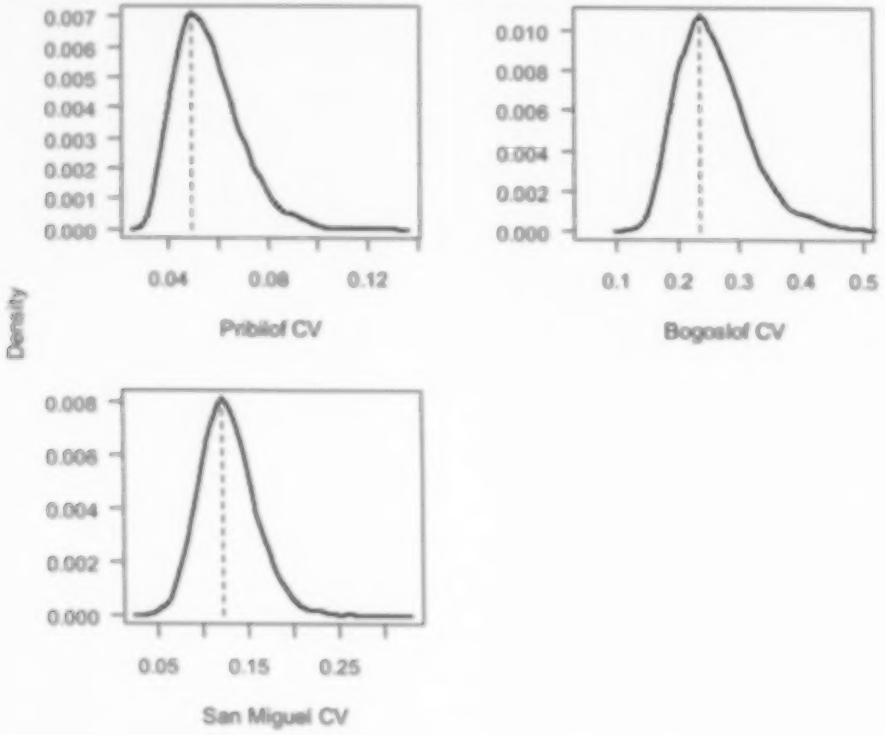
Fig. 8. Posterior probability distributions of estimated observation error coefficient of variation (CV) parameters for the model with the lowest deviance information criterion (DIC) score, which allows Bogoslof Island and San Miguel Island to each have unique observation error CVs. The Pribilof Islands have the lowest observation error, while Bogoslof Island appears to have the largest observation error. The broken vertical line represents the posterior mode of each distribution.



be non-zero. Our mixture model could still be applied to such data, but results would have to be interpreted differently. Instead of interpreting the process error mixture as the error for normal and catastrophic years, the mixture might be interpreted as a measure of data quality. In this setting, some small fraction of the data would be treated by the model as outliers, and those data points would be assigned to the component of the mixture associated with higher, larger variance (Chen and Fournier 1999). For each data set, researchers should consider the relationship of catastrophic parameters, magnitudes of observation, and process errors on power. A second potential criticism of the model is that the exponential or logistic population dynamics models in this analysis are too simple to represent reality. For many species, data that would allow the use of age-structured models have only been collected recently (Holmes and Fagan 2002). A potential future application of the catastrophic state–space model would be to apply it to age-structured data, with catastrophes only affecting one particular age class (e.g., juvenile survival).

In this paper, we demonstrate the application of a novel technique to estimate the probability of catastrophes. Estimation of catastrophes is important in both basic analyses of population dynamics and in applied analyses of extinction risk. Our analyses demonstrate the potential application of our approach in a meta-analysis, and similar studies should be conducted for taxa for which data are available for multiple populations. Our catastrophe model is able to incorporate catastrophes that affect total population size or specific components of the population (as in the fur seal example presented here). Although we cannot identify the cause for catastrophic events in the three time series of northern fur seal pups, the DIC weights provide strong support for the state–space model that includes catastrophes. It is not surprising that in the best model, there are large differences between the estimated CVs for each island. Because the Pribilof surveys involve multiple counts, they are more precise than direct counts from other islands (essentially a minimum estimate). The modes of the posterior distributions indicated that catastrophes occur on San Miguel with a 7.2% probability, and the average magnitude of those catastrophes is a 75% reduction in the number of pups. This estimated probability of a catastrophe is greater than the estimates previously suggested by Gerber and Hilborn (2001) for all otariid species.

In applying model selection tools such as DIC, it is important to stress the fact that even though the catastrophic model received the majority of the model weights, none of the models in this analysis should be considered the true model. As our simulations illustrated, the power to detect catastrophes is strongly affected by observation error and both the frequency and magnitude of the catastrophic events. Process error also appears to have an effect on power, but increasing the magnitude of the process error also increases

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the chance of falsely detecting catastrophes. Under the range of errors and catastrophic parameters that affect *C. ursinus* populations and surveys, the power to detect catastrophes is greater than chance alone, but probably in the range of 80%–90%. These results underscore the importance of quantitative analyses to determine data needed to detect catastrophes. Data requirements are expected to differ both between species and between population dynamics models — if the model were to be extended to include catastrophes in age-structured population dynamics, a single, annual abundance estimate for each population would likely not be sufficient.

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Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts

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Abstract: Two measures of productivity for fish stocks (recruitment and stock–recruit residuals) within two large marine ecosystems (Gulf of Alaska and eastern Bering Sea – Aleutian Islands) showed significant positive covariation within several groups of species and significant negative covariation between certain others. For example, stock–recruit residuals of gadids (Gadidae) in the Bering Sea were inversely related to those of shelf flatfishes (Pleuronectidae), suggesting that environmental forcing affects these groups in opposite ways. Salmon (*Oncorhynchus* spp.), Pacific herring (*Clupea pallasii*), and groundfish stocks each showed strong patterns of covariation within these taxonomic groups and within ecosystems, and both salmon and groundfish stocks showed positive covariation between the two ecosystems. However, we found little evidence of covariation between salmon and herring stocks or between these stocks and demersal stocks. Recruitment and stock–recruit residuals in individual stocks did not show a consistent response to known climatic regime shifts. However, combined indices of productivity across stocks showed decadal-scale variability (regime-like patterns), suggesting that both pelagic productivity (mostly salmon) and demersal productivity increased in response to the well-documented 1976–1977 climatic regime shift, whereas the 1988–1989 regime shift produced inconsistent or short-lived responses.

Résumé : Deux mesures de la productivité des stocks de poissons (résidus du recrutement et des stocks–recrues) dans deux grands écosystèmes marins (golfe d'Alaska et est de la mer de Bering – îles Aléoutiennes) affichent une covariation positive significative chez plusieurs groupes d'espèces et une covariation négative significative chez certains autres. Par exemple, les résidus stocks–recrues des gadidés (Gadidae) de la mer de Bering sont en relation inverse avec ceux des poissons plats du plateau continental (Pleuronectidae), ce qui laisse croire que le forçage environnemental affecte ces groupes de manière inverse. Les stocks de saumons (*Oncorhynchus* spp.), de harengs (*Clupea pallasii*) et de poissons de fond montrent tous de forts patrons de covariation à l'intérieur de ces groupes taxonomiques et au sein des écosystèmes; les stocks de saumons et de poissons de fond montrent tous les deux une covariation positive entre les deux écosystèmes. Nous ne trouvons que peu d'indication de covariation entre les stocks de harengs et de saumons ou entre ces stocks et les stocks benthiques. Les résidus du recrutement et des stocks–recrues dans les stocks individuels n'offrent pas de réponse uniforme aux changements connus du régime climatique. Cependant, les indices combinés de productivité dans tous les stocks montrent une variabilité (patrons typiques d'un régime) à l'échelle de la décennie; cela indique que la productivité pélagique (surtout du saumon) et la productivité profonde ont augmenté toutes les deux en réaction au changement de régime climatique bien étudié de 1976–1977, alors que le changement de régime de 1988–1989 a produit des réactions irrégulières ou de courte durée.

[Traduit par la Rédaction]

Introduction

The abundance and productivity of commercial fish stocks varies on interannual and interdecadal time scales as a result of environmental variations, species interactions, and fishing. Although the relative magnitude of these effects is not known, it is widely believed that environmental conditions have a dominant influence on productivity of fish populations in the Northeast Pacific Ocean through bottom-up forcing (e.g., Francis et al. 1998). Large-scale patterns of environmental variability and decadal-scale regime shifts in the Northeast Pacific appear to coincide with changes in many biological communities (Hare and Mantua 2000). For example, shifts in the mean state of the Pacific Decadal Oscillation (PDO), the dominant pattern of sea-surface temperature variability over much of the 20th century (Mantua and

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Hare 2002), correspond to similar shifts in catches of several salmon species (*Oncorhynchus* spp.) aggregated across large areas (Hare and Francis 1995). Similarly, variability in recruitment of many groundfish (demersal) stocks in the Northeast Pacific is characterized by synchronous strong year classes, with timing and frequency that appear to be related to interannual and decadal-scale variations in sea-surface temperature, which is in turn related to El Niño and decadal-scale variability (Hollowed and Wooster 1995; Hollowed et al. 2001). Field and Ralston (2005) also documented substantial spatial synchrony in recruitment within each of three rockfish species (*Sebastes* spp.) across locations of up to about 1000 km in the California Current system, but they did not use environmental data to interpret the observed synchrony.

Previous studies have also found regional-scale synchronicity within species for herring and salmon stocks in the Northeast Pacific. In contrast to many recent studies that have focused on large-scale climate variability at decadal time scales, stock-specific survival rates of salmon from spawners to adults tend to be dominated by interannual variability and show positive covariation among stocks at smaller spatial scales of only a few hundred kilometres (Peterman et al. 1998; Botsford and Paulsen 2000; Pyper et al. 2001). These salmon survival rates are more strongly related to local or regional-scale variability in coastal sea-surface temperatures during early ocean life than to large-scale indices such as the PDO (Mueter et al. 2002*a*). Similarly, recruitment of Pacific herring (*Clupea pallasi*) stocks in British Columbia, southeastern Alaska coastal waters, the outer Gulf of Alaska, and the Bering Sea is positively correlated within each of these four regions but is largely uncorrelated between regions (Williams and Quinn 2000). Herring and salmon recruitment in the Bering Sea and Gulf of Alaska typically increase with increasing coastal ocean temperatures, whereas recruitment of more southern stocks from British Columbia (B.C.) and Washington is reduced by high coastal sea-surface temperatures during the early ocean life phase (Williams and Quinn 2000; Mueter et al. 2002*a*), implying that synchronous changes in coastal temperatures affect recruitment of southern and northern stocks in opposite ways.

The observation that catches, recruitment, or survival rates of numerous pelagic and demersal fish stocks are linked to local and large-scale variability in sea-surface temperature suggests that widespread covariation or synchronicity in productivity might also occur across species as a result of shared environmental forcing and its influence on productivity of lower trophic levels. Positive covariation is apparent in long-term catch trends of different Pacific salmon species (Beamish and Bouillon 1993; Hare et al. 1999) and in the appearance of synchronous strong year classes in major Northeast Pacific groundfish populations (Hollowed and Wooster 1995; Hollowed et al. 2001). However, the magnitude and spatial scale of covariation across different species in the North Pacific has rarely been quantified. Notable exceptions are Botsford and Lawrence (2002) for Dungeness crab (*Cancer magister*) and Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon, Pyper et al. (2005) for sockeye (*O. nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon, and Field and Ralston (2005) for three rockfish species.

To improve our understanding of how climate variability affects different fish populations within species, as well as across species, in the Northeast Pacific, we conducted a comprehensive analysis of covariation patterns among groundfish, salmon, and herring stocks off Alaska. Our goal was to quantify the spatial extent of covariation in productivity, as measured by recruitment or survival rate indices (stock–recruit residuals, which can be interpreted as survival rates adjusted for density dependence), among major commercial fish stocks in the Bering Sea – Aleutian Islands and the Gulf of Alaska ecosystems (Fig. 1). Specifically, we examined time series of recruitment and survival rate indices for the presence of either positive or negative covariation among stocks within each ecosystem and between ecosystems. In addition, we examined trends in the indices for individual stocks and across stocks within each ecosystem for evidence of decadal-scale variability and abrupt shifts in the mean state of an index. Our general hypotheses included (1) recruitment–survival of different demersal stocks within the two regional ecosystems do not vary independently; (2) recruitment–survival of demersal stocks is correlated between ecosystems; (3) recruitment–survival of salmon and herring stocks varies independently from that of demersal stocks; (4) temporal variability in recruitment–survival is dominated by decadal-scale patterns; and (5) abrupt shifts in mean recruitment or survival occur more frequently than expected by chance. Each of these hypotheses was tested against the null hypothesis of no significant correlations among time series of productivity (hypotheses 1–3) or no significant temporal trends in productivity series (hypotheses 4–5).

Materials and methods

Data sources

We compiled data from various agencies and researchers. Time series of spawning biomass and recruitment for 23 stocks of groundfish from the Bering Sea and Aleutian Islands region (BSAI, 11 stocks) and Gulf of Alaska (GoA, 12) were obtained from 2005 stock assessments (Table 1). Recruitment estimates for recent years were not included if deemed unreliable by management agency authors of the assessment. Spawner abundances and number of recruits by ocean-entry year were obtained for 14 regional stock groups of sockeye (4 groups), pink (5), and chum (5) salmon between northern British Columbia and western Alaska (Table 1). The number of spawners and recruits of pink and chum salmon were combined across stocks within regions for which there was strong within-species positive covariation in survival rates, as identified in Pyper et al. (2001). Spawner and recruit data for sockeye salmon stocks were similarly combined within regions as summarized in Table 1. Salmon within each of these regions were treated as a single stock (or "stock group") in the analysis. We obtained time series of spawning stock biomass and recruitment for 13 herring stocks from Williams and Quinn (2000) and used these to describe spatial covariation among herring stocks. Because these time series had little overlap with some of the salmon and groundfish stocks, we used updated time series

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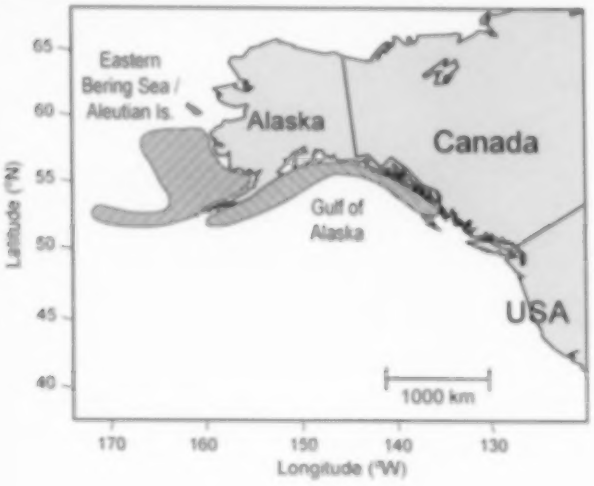
Fig. 1. Map of Northeast Pacific showing the Bering Sea – Aleutian Islands and the Gulf of Alaska ecosystems (hatched areas).



of spawning biomass and recruitment for the Togiak herring stock, for Prince William Sound herring, and for several Southeast Alaska herring stocks combined (Table 1) in the analysis of covariation. All demersal stocks included here, with the exception of sablefish and Pacific halibut, are assessed and managed as a unit stock within one of the two ecosystems. The sablefish stock ranges throughout the GoA and into the BSAI region but was assigned to the GoA ecosystem because 91% of total Alaskan sablefish catches over the last decade (1993–2002) occurred within the GoA. Pacific halibut are assessed separately within different regions, but we included only the GoA portion of the stock (International Pacific Halibut Commission regulatory areas 2B, 2C, and 3A combined) because time series in the BSAI were too short for our analysis.

Indices of fish productivity

We used two different measures of productivity in our analyses: (*i*) log-transformed recruitment estimates (log R, using natural logarithm) and (*ii*) stock–recruit residuals (SR index) from the best-fit stock–recruitment model as defined below. Recruitment of groundfish and herring stocks was simply the estimated number of recruits at the youngest age that was estimated in age-structured assessment models. Age at recruitment varied from age 1 to age 6 (Table 1). Recruitment of salmon stocks was estimated as the total number of salmon from a given brood (spawning) year that survive to either be caught in the fishery or escape to spawn (for further details, see data sources in Table 1). All recruitment estimates were log-transformed to reduce the influence of exceptionally strong year classes and to obtain an index that is more appropriate in correlation analyses, which can be sensitive to outliers. The SR index was obtained for each of the stocks or stock groups listed in Table 1 by computing residuals from a stock–recruitment model that was fit to time series of recruits resulting from parental spawning in year t (R_t) and the corresponding spawner abundance or biomass (S_t). Models were fit on a log scale with log(survival), i.e., $\log(R_t/S_t)$, as the dependent variable and S_t as the independent variable (see below). This has the effect of removing presumed density-dependent effects of spawner abundance on survival rates; hence, the SR index reflects unexplained variability in recruitment resulting from environmental fluctuations and measurement errors (e.g., Peterman et al. 1998).

Because the form of the stock–recruitment relationship is unknown and may vary among stocks, we fit several models to each spawner–recruit series, including the two-parameter Ricker and Beverton–Holt (BH) models. Functional forms and parameter estimation routines are described in Quinn and Deriso (1999). Models assumed a multiplicative, lognormal error structure and took the following general form:

$$\log(R_t/S_t) = f(S_t) + \varepsilon_t$$

where $f()$ denotes a function describing the stock–recruitment relationship on the log-transformed scale and ε_t denotes the normally distributed residual for year t. Residuals were assumed to be either independent and identically distributed or first-order autocorrelated (see below), and S_t was assumed to be known without error. Models were fit using linear (Ricker) or nonlinear (BH) least-squares regression.

Annual stock–recruit residuals are often not statistically independent and we tested for significant autocorrelation by fitting autoregressive models ranging from order 0 (independent observations) to order 6 (up to 6-year "memory") to each residual series. With few exceptions, residuals were independent or were best approximated by a first-order autoregressive process. Therefore, to account for time-series dependence in log(survival), we fit each of the models with and without first-order autocorrelation ($\varepsilon_t = \phi_1 \varepsilon_{t-1} + \nu_t$, where ϕ_1 is the first-order autoregressive coefficient and $\nu_t \sim N(0, \sigma_\nu^2)$). Models with autocorrelated residuals were fit using a linear or nonlinear generalized least-squares approach as implemented in S-Plus (Pinheiro and Bates 2000). The statistically best model for each stock was selected from the set of four different models (Ricker and BH models with or without first-order autocorrelation) based on the small-sample Akaike information criterion (AIC_c; Hurvich and Tsai 1989). We then used residuals from the model with the lowest AIC_c score as our final SR index in further analyses.

To compare recruitment and stock–recruit residuals among stocks and to estimate the magnitude of covariation, we aligned all indices (log R and SR) by year class, which was defined as the larval stage (age 0) for groundfish and herring and as the year of ocean entry (outmigration) for juvenile salmon. The larval stage was used for groundfish and herring because much of the variability in survival and recruitment is generally believed to be determined during early life stages. However, by aligning stocks in this manner, the mechanisms that induce covariation among stocks may occur at any life stage, as long as they occur at the same stage in different species. Ocean-entry year was used for salmon because much of the variability in overall spawner-to-recruit survival is due to variability during the early ocean phase (Peterman 1987; Pyper et al. 2005) and because it is the only time when juvenile salmon share the coastal environment with early life stages of nonsalmonid coastal marine species. Pink and chum salmon enter the coastal ocean at age 1 year, sockeye salmon from B.C. enter the ocean at age 2, and all

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Table 1. Stocks and stock groups used in analyses by species and region (BSAI, Bering Sea – Aleutian Islands; GoA, Gulf of Alaska; cGoA, central Gulf of Alaska; wGoA, western Gulf of Alaska, etc.; PWS, Prince William Sound; SEAK, Southeast Alaska; nBC, northern British Columbia), range of year classes for which both spawner and recruitment data were available, age for recruitment as specified in age-structured assessment models, the best stock–recruitment model (BH, Beverton–Holt), the autoregressive coefficient (ϕ_1) for residuals from the stock–recruitment model, if significant at $\alpha = 0.05$, proportion of deviance (% Dev.) explained by decadal-scale trends, associated *p* values, and significant trends in log *R* and SR series.

Scientific name	Common name	Region	Year classes	Age	Model	ϕ_1	% Dev.	*p* value	Linear trend	
									log *R*	SR
Atheresthes stomias	Arrowtooth flounder	BSAI[a]	1976–2001	2	BH		40.0	0.053	+	
		GOA[b]	1961–2001	3	BH	0.89	**59.2**	**<0.001**	+	
Hippoglossoides elassodon	Flathead sole	BSAI[a]	1977–2002	3	Ricker		14.3	0.674	–	
		GOA[b]	1984–2001	3	Ricker		22.9	0.460		
Reinhardtius hippoglossoides	Greenland turbot	BSAI[a]	1974–2001	1	Ricker	0.95	**77.6**	**<0.001**		
Hippoglossus stenolepis	Pacific halibut	GOA[c]	1974–1999	6	Ricker		26.3	0.257	+	
Limanda aspera	Yellowfin sole	BSAI[a]	1964–2000	5	Ricker		36.0	0.052	–	
Lepidopsetta sp.	Rock sole	BSAI[a]	1975–1999	4	Ricker	0.51	**56.8**	**0.004**		
Pleuronectes quadrituberculatus	Alaska plaice	BSAI[a]	1975–2001	3	BH		**44.4**	**0.022**	–	–
Glyptocephalus zachirus	Rex sole	GOA[b]	1982–2001	3	Ricker		**46.7**	**0.040**		
Microstomus pacificus	Dover sole	GOA[b]	1984–2001	3	Ricker		6.8	0.913		
Theragra chalcogramma	Walleye pollock	BSAI[a]	1964–2003	1	Ricker		19.5	0.476		
		GOA[b]	1969–2003	2	BH	0.56	**51.1**	**0.004**	–	–
Gadus macrocephalus	Pacific cod	BSAI[a]	1964–2003	0	BH	0.38	**55.2**	**<0.001**		
		GOA[b]	1964–2003	0	BH	0.35	**47.7**	**0.005**		
Pleurogrammus monopterygius	Atka mackerel	BSAI[a]	1977–2002	1	Ricker		35.6	0.094		
Anoplopoma fimbria	Sablefish	GOA[b]	1960–2003	2	Ricker		16.4	0.668		
Sebastes alutus	Pacific ocean perch	BSAI[a]	1960–1994	3	BH		**47.6**	**0.008**		
		GOA[b]	1961–2001	2	BH	0.56	31.6	0.085	+	
Sebastes polyspinis	Northern rockfish	BSAI[a]	1977–1994	3	Ricker		25.8	0.385		
		GOA[b]	1977–1999	2	Ricker		19.1	0.351		
Sebastes variabilis	Dusky rockfish	GOA[b]	1977–2001	4	Ricker		**68.1**	**<0.001**		
Sebastes aleutianus	Rougheye rockfish	GOA[b]	1977–2001	3	Ricker		17.3	0.565	+	
Oncorhynchus nerka[d]	Sockeye salmon	BSAI	1959–1996		Ricker	0.61	**67.6**	**<0.001**		
		wGoA	1953–1996		Ricker		17.2	0.550	+	
		cGoA	1973–1994		Ricker		27.0	0.227	+	
		nBC	1969–1993		BH		23.4	0.364	+	+
Oncorhynchus keta[e]	Chum salmon	BSAI	1979–1993		BH		37.6	0.144		
		wGoA	1963–1993		BH	0.59	**53.5**	**0.003**	+	
		cGoA	1973–1993		BH		**52.5**	**0.014**	–	–
		PWS	1967–1994		BH	0.56	**66.1**	**<0.001**		
		nBC	1966–1993		BH		17.9	0.605		
Oncorhynchus gorbuscha[f]	Pink salmon	wGoA	1963–1996		BH	0.60	**58.8**	**0.001**	+	+
		Kodiak	1963–1997		Ricker		15.4	0.672	+	
		cGoA	1972–1997		BH		27.7	0.224		
		SEAK	1961–1997		BH	0.34	**39.2**	**0.029**	+	+
		nBC	1951–1996		Ricker		20.6	0.406		

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Table 1 (*continued*).

Scientific name	Common name	Region	Year classes	Age	Model	ϕ_1	% Dev.	*p* value	Linear trend log *R*	Linear trend SR
Clupea pallasi	Pacific herring	BSAI[f]	1977–2001	4	BH		**67.2**	**<0.001**		-
		PWS[g]	1980–2002	3	BH		20.7	0.512		
		SEAK[i]	1980–2000	3	BH		17.8	0.504		

Note: Year classes for salmon denote year of ocean entry. The percent deviance explained (% Dev.) is an estimate of the proportion of variability in stock–recruit residuals accounted for by decadal-scale trends (see text), and the associated *p* value denotes the significance of decadal-scale patterns relative to a constant mean model, based on an approximate χ^2 test. Boldface cases are significant at the 0.05 level. Significant ($p < 0.05$) positive (+) and negative (–) linear trends in log recruitment (log *R*) and stock–recruit residuals (SR) are based on a generalized least-squares regression with first-order autocorrelated residuals. All *Oncorhynchus* and *Clupea* species are referred to in the text as "pelagic" stocks; all others are "demersal" stocks.

[a]Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea - Aleutian Islands regions, North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99501, USA.

[b]Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501, USA.

[c]Stephen Hare, International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98145-2009, USA (personal communication).

[d]Individual sockeye stock data sets are from Peterman et al. (1998) and Mueter et al. (2002*b*). Stocks were combined within the Bering Sea (eight Bristol Bay stocks, Nayakik excluded because of missing years), western GoA (Black and Chignik lakes), central GoA (four stocks from Kodiak Island, Cook Inlet, and Copper River), and Northern B.C. (Skeena and Nass rivers). Outmigration was assumed to occur at age 3 for Alaska sockeye stocks and age 2 for stocks in British Columbia.

[e]Chum salmon data based on Pyper et al. (2002). Data were combined by region within the Bering Sea (Bristol Bay, Yukon, and Norton Sound stocks), western GoA (Alaska Peninsula and Chignik), central GoA (Kodiak and Cook Inlet), Prince William Sound, and northern British Columbia.

[f]Pink salmon stocks were combined within five regions based on fig. 5 in Pyper et al. (2001), excluding Norton Sound and Washington stocks.

[g]Fred West, Alaska Department of Fish and Game, Anchorage, Alaska (personal communication).

[h]Steve Moffit, Alaska Department of Fish and Game, Cordova, Alaska (personal communication).

[i]Sherri Dressel, Alaska Department of Fish and Game, Juneau, Alaska (personal communication), sum of all Southeast Alaska stocks.

sockeye salmon smolts from Alaska were assumed to enter the ocean at age 3.

Data analysis

We describe patterns of variability and covariation in productivity of Northeast Pacific fish stocks by several methods, as detailed below: (*i*) examining the frequency distribution and temporal variability of log *R* and SR indices; (*ii*) quantifying the spatial scales of covariation among salmon stocks and among herring stocks, as well as between salmon and herring stocks, based on pair-wise correlations among log *R* or SR indices; (*iii*) testing for significant covariation between pelagic (salmon and herring) and demersal stocks within both ecosystems and among different demersal stocks within and between ecosystems (Fig. 2); (*iv*) identifying clusters of demersal stocks that showed similar patterns of variability; (*v*) developing combined indices of variability in log *R* and SR across all demersal stocks and across all pelagic stocks within a given ecosystem; and (*vi*) identifying significant change points (years with a significant step change) in log *R* and SR time series for individual stocks, stock clusters, and ecosystems.

Frequency distribution and temporal variability

The distribution of each log *R* and SR series was examined for univariate outliers, which may have an undue influence in the analysis of trends. Because outliers (>2.5 standard deviation, SD, from the mean) existed in some series, we repeated the trend analyses with these outliers excluded. We examined temporal variability in log *R* and SR indices to quantify the extent of autocorrelation and the magnitude of interannual variability relative to long-term, decadal-scale trends. Covariation in productivity among stocks may be due to shared variability at interannual scales or at longer, e.g., decadal, scales. To quantify the magnitude of interannual- and decadal-scale variability, we fit nonparametric smoothing splines (cubic B-spline smoother) to each of the time series (Hastie and Tibshirani 1990) and computed the proportion of overall variability that was attributable to decadal-scale trends as the proportion of overall deviance explained by the smooth fit. The deviance is a likelihood ratio statistic for generalized linear and additive models that is roughly equivalent to the coefficient of determination in linear models (see, e.g., Hastie and Tibshirani 1990). Smoothing splines were constrained to have approximate degrees of freedom (df) in proportion to the length of each time series (df = 27/10 years, where *T* is the number of years in the series). Although the degree of smoothing was arbitrary, the denominator (10 years) ensures that if there is a trend in the smoothed series, it will roughly correspond to the decadal-scale variability that is dominant in many biological and physical time series in the Northeast Pacific (Hare and Mantua 2000). By fixing the degree of smoothing across time series of equal length, we ensured that the proportion of variability accounted for by smooth trends was comparable across series. However, the shape of the smooth functions could vary greatly between series. For each time series, we tested whether a decadal-scale trend based on smoothing splines provided a significantly better fit than a constant mean model, using an approximate χ^2 test (Wood 2000). In addition, we tested whether significant lin-

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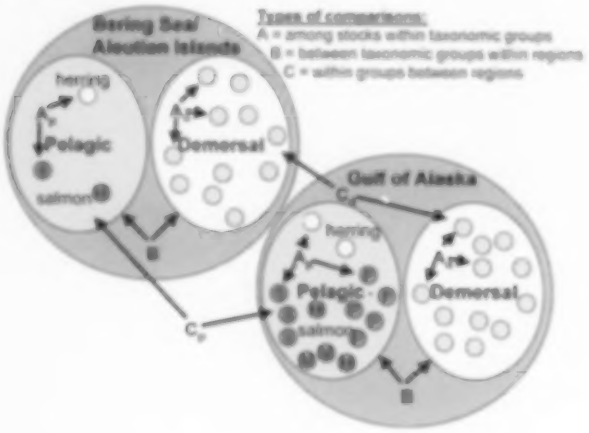
Fig. 2. Schematic of types of comparisons among different groups of species within and between the Gulf of Alaska and Bering Sea – Aleutian Islands. Each stock is depicted by a small circle. Salmon stocks include sockeye (S), chum (M), and pink (P) salmon.



ear time trends were present in the time series by fitting generalized least squares regressions that allowed for first-order autocorrelated residuals to each log R and SR series.

Spatial scales of covariation of salmon and herring stocks

Spatial scales of covariation among different salmon species are quantified in Pyper et al. (2005). We used the same approach to quantify the spatial scale of covariation among SR indices of 13 herring stocks. We first computed Pearson's product-moment correlations between each pair of log R (or SR) series based on all years that had data for both series in a given pair. Although trend removal or prewhitening is sometimes used before computing correlation to focus on covariation at interannual scales, we computed correlations among "raw" (rather than detrended) indices. Therefore, the patterns of covariation described here reflect shared variability among stocks at all time scales. Bivariate outliers may have a strong influence on pair-wise correlations and could lead to erroneous conclusions. Therefore, we used two methods to guard against such errors. First, we computed Spearman's rank correlations, which are not affected by outliers, and compared results with the analysis of Pearson's correlations. Second, we examined scatterplot matrices of all pairs of indices for potentially influential outliers. These analyses revealed several influential observations that were evident both in individual series and in bivariate scatterplots. Eliminating these observations or using rank-based correlations resulted in larger absolute correlations and would have strengthened our conclusions. Because there was no a priori reason to exclude these observations, we show results based on Pearson's product-moment correlations with all observations included.

We described the spatial extent of covariation among herring stocks by plotting pair-wise correlations between log R (or SR) series of different stocks as a function of the geographical distance separating their centers of distribution. Average correlations at a given separation distance were estimated by fitting a nonparametric covariance function (Bjørnstad and Falck 2000) to the observed correlations as a function of distance. Similarly, we computed pair-wise correlations between the SR indices of all salmon stocks for a given species (sockeye, pink, or chum salmon) and the SR indices of herring stocks. To estimate average correlations between SR indices of herring and salmon stocks by distance, we fit a nonparametric covariance function to the relationship between the observed pair-wise correlations and the geographical distance separating the ocean entry point of a given salmon stock from the center of distribution of a given herring stock.

Covariation patterns of demersal and pelagic stocks

Unlike herring and salmon, which can be divided into multiple regional stocks, the demersal species examined here typically consist of a single management unit and (or) biological population (i.e., a single stock) within a given ecosystem. Therefore it was not possible to describe spatial patterns of covariation within a species as a function of distance using covariance functions. Instead, we examined covariation among different demersal stocks or species within and between ecosystems (comparisons A_d and C_d, respectively, in Fig. 2) and between demersal and pelagic stocks within each ecosystem (comparisons B in Fig. 2). To summarize correlations among log R series of demersal stocks, we plotted frequency distributions (histograms) of all pair-wise correlations within and between ecosystems. Correlations among SR series were examined similarly. The observed correlations will differ from zero because of random variability and because of true covariation between stocks (positive or negative). Because we examined multiple pair-wise correlations, univariate tests are not appropriate to detect significant covariation. Instead, we evaluated whether the frequency distribution of pair-wise correlations differed from the expected distribution under the null hypotheses (H_0) that stocks vary independently, i.e., that log R (or SR) series for a given group of stocks (for example, all demersal stocks in the GoA) are independent of each other.

In the presence of significant covariation among stocks, the observed frequency distribution of correlations may differ from that expected under H_0 in at least two important ways. First, the average correlation ($\bar{r}$) may differ from zero. Second, correlations may be more dispersed than expected under H_0, implying both significant positive and significant negative covariation among stocks. To test whether $\bar{r}$ among a group of stocks significantly differed from zero, we used randomization tests to obtain the expected distribution of $\bar{r}$ under H_0. The randomization procedure was designed to account for autocorrelation in the time series and for observed within-group correlations when testing correlations between groups, as described in detail in Pyper et al. (2001). Specifically, we examined the following hypotheses with regard to covariation in productivity (as measured by log R or SR indices) within and between different groups of fish stocks. First, for both ecosystems (BSAI and GoA), we tested whether the average correlation between log R (or SR) indices across all pairs of demersal stocks was significantly different from zero (comparisons A_d in Fig. 2). Pelagic stock groups within each system were compared in the same way

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(comparisons A_p in Fig. 2). Second, we tested whether average correlations between indices for pelagic stocks in a given ecosystem and indices for demersal stocks in the same ecosystem were significantly different from zero (comparisons B in Fig. 2). Third, we tested whether average correlations among indices for demersal stocks from different ecosystems (i.e., groundfish stocks in the BSAI versus those in the GoA) were significantly different from zero (comparison C_d in Fig. 2). Pelagic stocks were compared between ecosystems in the same way (comparison C_p in Fig. 2). If, for any groups, average correlations were not significantly different from zero, we tested for significant overdispersion in the frequency distribution of all pair-wise correlations. Overdispersion implies larger absolute correlations ($|r|$) than expected under H_0 or, equivalently, a larger variance of the observed correlations (σ_r^2) than expected. Therefore, we compared the observed values of $|r|$ and σ_r^2 with those expected under the null hypothesis of no significant overdispersion. The expected distribution of $|r|$ and σ_r^2 under H_0 was obtained as part of the same randomization procedure that was used to test average correlations as described above and in Pyper et al. (2001). The tests for overdispersion are only valid if average correlations are not significantly different from zero because such a difference implies significantly higher absolute correlations (as can be easily verified through simulations).

Clustering of demersal stocks

To identify groups of demersal stocks that vary in similar ways within each ecosystem, we applied hierarchical clustering using Ward's minimum variance method and Euclidean distances (Kaufman and Rousseeuw 1990) to the log R and, separately, to the SR index series within each system. Pairwise Euclidean distances among the standardized series were computed using all years of overlap between the two component series of a given pair. To examine the sensitivity of results to the distance measure and clustering algorithm, we also used Manhattan distances (sum of absolute differences) and average linkage clustering with both Euclidean and Manhattan distances. Results based on different clustering algorithms were examined for consistency. If consistent clusters were identified, we combined the log R (or SR) series within each cluster by standardizing each series (zero mean and unit variance) and computing the mean across series to obtain a single time series of log R (or SR) indices for each cluster. The resulting time series characterize variability in recruitment or survival rates of the major groups of positively covarying species. We assume that positive covariation results from shared environmental influences on recruitment or survival rates; hence combining series may provide a clearer "signal" of the underlying environmental influences than that provided by individual time series, which are more variable because of random observation errors.

Combined indices of recruitment and survival rate

In addition to stock-specific and cluster-specific indices of productivity, we combined log R and SR across all demersal and pelagic stocks within the BSAI and GoA, respectively. Each time series of log R indices was first standardized and indices were averaged for a given year class across all demersal or pelagic stocks in an ecosystem. SR indices were combined in the same way. The combined or aggregated log R and SR indices thus give equal weight to each stock rather than weighting by abundance, which would have resulted in indices that are dominated by the most abundant species. We obtained four combined log R indices and four combined SR indices consisting of two indices of demersal productivity (one for each ecosystem) and two indices of pelagic productivity. Although we averaged across different series that may have fluctuated independently or even in opposite ways, the combined standardized indices reflect whether recruitment and survival rates were generally above or below average across the most important commercial species. Before standardizing individual series, "missing" values at the beginning and end of each series were estimated by regression imputation, which exploits the correlation structure among series to estimate missing values and assumes that this correlation structure is the same throughout the time series (Schafer 1997). Missing values were only estimated if log R or SR values were available for at least 50% of the stocks in a given year and only for year classes between 1970 and 2001. Filling in missing values adds uncertainty to the combined, or averaged, indices. To account for this uncertainty, we obtained multiple imputations through bootstrap resampling from the full distribution of imputed values (2000 replicates), averaged the stock-specific indices resulting from each imputation, and constructed 95% confidence intervals based on the frequency distribution of these averages across multiple imputations.

Change point analysis

We examined stock-specific and ecosystem-specific time series of log R and SR indices using a "sequential t test analysis of regime shifts" (STARS; Rodionov and Overland 2005). The STARS method sequentially tests whether each data point in a time series is significantly different from the mean of data points representing the latest "regime". The last data point in a time series may be identified as the beginning of a new "regime", and as more data are added to the time series, this is confirmed or rejected. The STARS method requires the prior specification of a cutoff value (minimum number of years in a regime) and a p value (probability level). For this analysis, we chose a cutoff value of 10 years and a p value of 0.1. The analysis was completed for a range of cutoff values (5, 7, 10, 15, 20) and two p values (0.05, 0.1). The results from each combination of these parameter values were compared, and we found that a cutoff value of 10 and a p value of 0.1 consistently captured the majority of shifts that were captured by other combinations of parameter values. Results for other combinations of parameter values differed primarily because of shifts found near the ends of certain time series and additional shifts found in some highly variable series.

We applied the STARS analysis across all demersal stocks (Bering Sea and Gulf of Alaska combined) and across all pelagic stocks, respectively, and measured the evidence for a significant shift in any given year across all stocks based on the "regime shift index" (RSI) of Rodionov and Overland (2005). The RSI was computed for each stock and was averaged separately across demersal and pelagic stocks. There-

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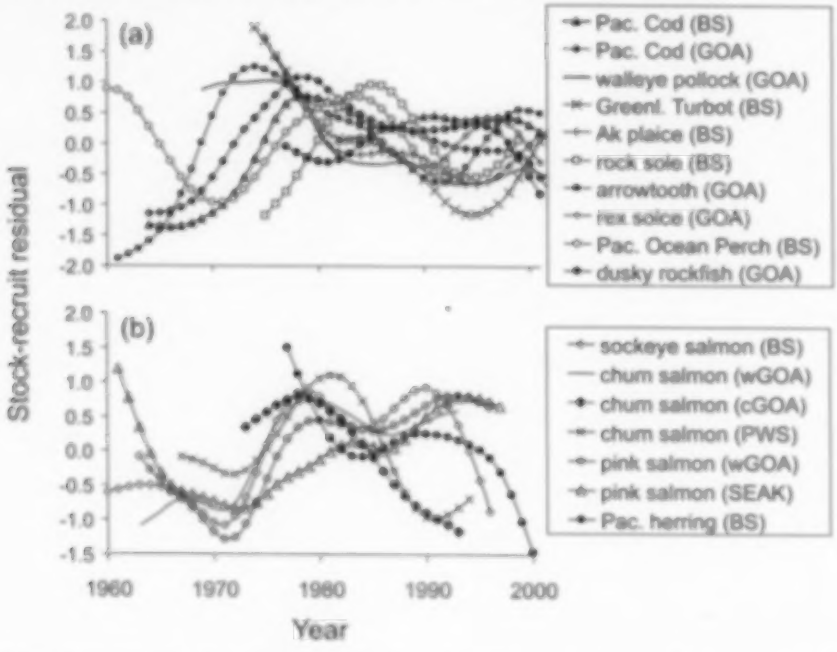
Fig. 3. Smoothed trends (cubic B-spline smoother) in stock–recruit residuals (SR indices) for (*a*) six groundfish stocks and (*b*) eight pelagic stocks that had significant ($p < 0.05$) decadal-scale trends. Pac., Pacific; Ak, Alaska; BS, Bering Sea; GOA, Gulf of Alaska; wGOA, western GOA; cGOA, central GOA; PWS, Prince William Sound; SEAK, Southeast Alaska.



fore, a large average RSI may result from a pronounced shift in one or a few series or from small shifts in many individual series. In addition, we applied the STARS analysis to each of the combined, ecosystem-wide log *R* and SR indices to test for significant shifts in these combined indices.

Results

Frequency distribution and temporal variability

Time series of both log *R* and SR indices were typically close to normally distributed, but one or more outliers (>2.5 SD from the mean) were present in some series. However, the influence of these outliers on the trend analysis was generally negligible, and eliminating individual outliers did not change the overall conclusions. Therefore, all results are presented without excluding outliers.

Most of the time series of log *R* and SR indices could be well approximated by either a white-noise series or a first-order autoregressive series. First-order autoregressive coefficients for the stock–recruit residuals were generally positive and were significant ($p < 0.05$) for 12 out of 40 stocks, with significant autoregressive coefficients ranging from 0.34 to 0.95 (Table 1). Strong autocorrelation in stock–recruit residuals was evident in several rockfish and salmon stocks and in the GoA stocks of walleye pollock and Pacific cod (but not, or to a much lesser extent, in the BSAI stocks of these species). In addition, we found strong autocorrelation in the log *R* series of most flatfish stocks. However, after accounting for effects of spawner biomass on flatfish recruitment, autocorrelation in the SR indices was no longer significant in most cases, except for arrowtooth flounder in the GoA and Greenland turbot and rock sole in the BSAI (Table 1).

Ten out of 23 demersal stocks and 7 out of 17 pelagic stocks showed significant evidence of decadal-scale variability in stock–recruit residuals, with most of those showing greater than 50% of the deviance accounted for by decadal-scale smoothed trends (Table 1). Although patterns of decadal-scale variability differed among species, several common trends emerged (Fig. 3). Stock–recruit residuals of the demersal stocks with significant trends typically increased in the 1970s, peaked in the late 1970s or early 1980s, and were relatively low in the 1990s. Almost all of the salmon stocks were characterized by strongly negative stock–recruit residuals, indicating unusually low survival rates, in the early 1970s, increasing to positive stock–recruit residuals in the late 1970s – early 1980s. Compared with SR indices, recruitment series showed similar patterns of variability but displayed more pronounced decadal-scale trends in some cases (e.g., flatfishes), presumably because of the effects of low-frequency variations in spawner abundance on recruitment.

An analysis of statistically significant linear time trends between 1970 (or the first year after 1970 with data) and the last year for which estimates were available suggested that recruitment and stock–recruit residuals of demersal stocks showed variable trends over this period, whereas those of salmon stocks generally increased (Table 1). Of nine demersal stocks with significant linear trends in log *R*, four stocks showed long-term decreasing trends in recruitment since 1970, whereas recruitment of five stocks increased over time (Table 1). Of 14 salmon stocks, the log *R* of seven

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stocks increased significantly from 1970 to the late 1990s, whereas only one stock (chum salmon in the central GoA) decreased significantly. Fewer SR than log R series showed significant trends over time, but they generally had the same sign as trends in log R for a given stock.

Spatial covariation of salmon and herring stocks

Average correlations between pairs of SR indices for salmon stocks of the same species (Fig. 4*a* and Mueter et al. 2002*b*) and for Pacific herring stocks (Fig. 4*c*) show moderate to strong positive covariation at regional spatial scales of up to several hundred kilometres but no evidence of significant correlations at larger spatial scales. The covariance function by distance for herring stocks was very similar in magnitude to that observed for pink salmon. The average correlation between nearby herring stocks was about 0.6 and decreased to less than 0.2 at about 1000 km. Average correlations among herring stocks were not significantly different from zero at distances larger than 1000 km. Similarly, stocks of different salmon species with ocean-entry points separated by less than a few hundred kilometres tended to be positively correlated (Fig. 4*b* and Pyper et al. 2005), whereas stocks that are separated by larger distances were on average uncorrelated. The largest between-species correlations were observed between SR indices of pink and chum salmon stocks with much weaker correlations between SR indices of sockeye salmon and either pink or chum salmon. We found no evidence of either positive or negative covariation between SR indices of herring and those of any of the salmon species (Fig. 4*c*), suggesting that the processes that determine survival of herring and salmon (as measured by SR indices) operate independently.

Covariation patterns of demersal and pelagic stocks

Based on average correlations among log R or SR indices, groundfish stocks within the BSAI and GoA showed relatively weak coherence. We found moderate but highly significant positive covariation among both log R and SR indices of the 12 demersal stocks in the GoA (Table 2) but little or no positive covariation, on average, among groundfish stocks in the BSAI. However, both the average absolute correlation and the variance across all pair-wise correlations in the 11 BSAI demersal stocks were much larger than expected by chance (hypotheses H_2 and H_3 in Table 2; Fig. 5), which implies that the magnitude of some correlations in the BSAI, both positive and negative, was higher than expected. This overdispersion resulted from two groups of species (flatfishes and gadids) with log R series, as well as SR series, that were positively correlated within groups but negatively correlated between groups (see clustering results below).

There was some positive covariation between demersal stocks in the BSAI and demersal stocks in the GoA, as evident in average correlations among log R indices and among SR indices that were significantly larger than zero (Table 2; Fig. 5). Positive covariation between groundfish in the two ecosystems was in part a result of covariation between stocks of the same species with log R and SR indices that were typically positively correlated between ecosystems. However, the correlations were significant for Pacific cod and Pacific ocean perch only ($p < 0.05$; Table 3) and were close to zero or negative for flathead sole and walleye pollock. Furthermore, there were numerous other positive correlations among specific stocks in the two systems that were significant ($p < 0.05$) but no significant negative correlations.

Finally, we found weak but significant positive covariation between log R (as well as SR) series of demersal and pelagic stocks in the GoA but not in the BASI region (Table 2). Positive covariation among demersal and pelagic stocks in the GoA resulted from positive correlations among the recruitment series of Pacific halibut, arrowtooth flounder, and several sockeye and pink salmon stocks. Correlations among

Fig. 4. Spatial correlation scales for salmon and herring stocks in the Northeast Pacific: (*a*) estimated average correlation between stocks of the same species as a function of the distance between ocean entry points for pink, chum, and sockeye salmon (modified from Mueter et al. 2002*b*); (*b*) estimated average correlations between stocks of different salmon species by distance (modified from Pyper et al. 2005); and (*c*) pair-wise correlations (circles) and average correlation by distance (heavy line) with 95% confidence interval (thin lines) for 13 herring stocks. Dotted lines in (*c*) denote pair-wise correlations by distance between herring stocks and sockeye, pink, and chum salmon stocks, respectively, none of which was significantly different from zero at any distance.

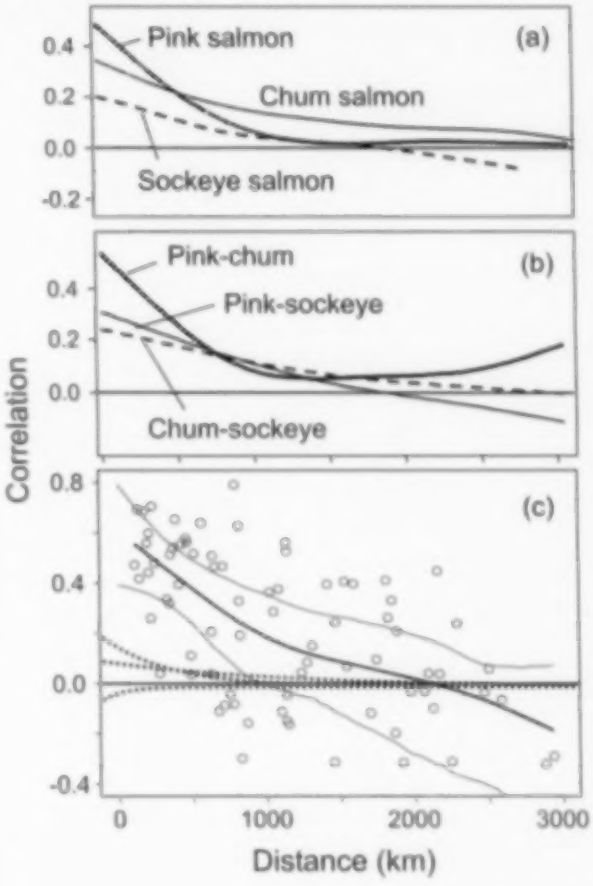

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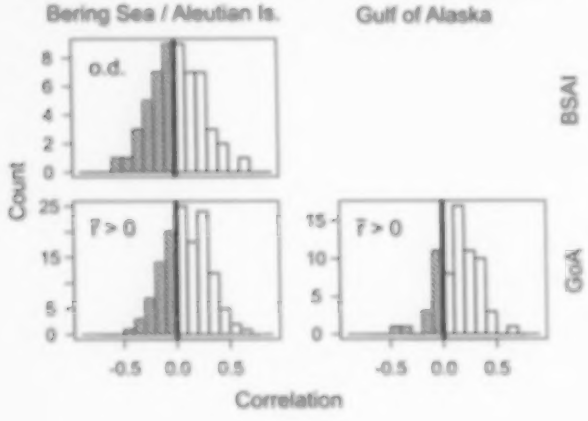
Table 2. Summary of results from randomization tests to test three hypotheses about within- and between-group correlations.

	log *R*					SR				
	$\bar{r}$	H_1 (p value)	$\|r\|$	H_2 (p value)	H_3 (p value)	$\bar{r}$	H_1 (p value)	$\|r\|$	H_2 (p value)	H_3 (p value)
Within-group correlations										
BSAI: 11 demersal stocks	0.029	0.155	0.22	0.012*	0.013*	0.033	0.132	0.195	0.088	0.065
GOA: 12 demersal stocks	0.176	<0.001***				0.203	<0.001***			
Between-group correlations										
BSAI vs. GoA: demersal	0.1	0.011*				0.11	<0.001***			
BSAI: demersal vs. pelagic	0	0.662	0.17	0.742	0.62	0	0.541	0.178	0.658	0.681
GoA: demersal vs. pelagic	0.12	0.003**				0.1	0.039*			

Note: We tested the overall hypothesis of independence of log recruitment (log *R*) or stock–recruit residuals (SR) of demersal stocks within or between each of two ecosystems and between demersal and pelagic stocks within a given ecosystem using three specific null hypotheses: H_1, the average correlation among stocks is zero ($\bar{r} = 0$); H_2, the average absolute value of correlations among stocks ($|r|$) is as expected under the assumption of independence ($|r|_{obs} = |r|_{exp}$); H_3, the variance of observed correlations is as expected under independence ($\mathrm{Var}(r_{obs}) = \mathrm{Var}(r_{exp})$). Within-group correlations were accounted for when testing correlations between groups. Significance: *, $p = 0.05$; **, $p = 0.01$; ***, $p = 0.001$.

Fig. 5. Histograms of all pair-wise correlations among stock–recruitment residuals (SR indices) of groundfish stocks within the Bering Sea – Aleutian Islands (BSAI, 11 stocks) and Gulf of Alaska (GoA, 12 stocks) (panels along diagonal) and between the BSAI and GoA (lower left panel). Hatched bars correspond to negative correlations. Results from randomization tests are indicated: $\bar{r} > 0$ means that average correlations are significantly larger than 0 ($p < 0.05$); o.d. means significant overdispersion.



the SR indices were weaker than among log *R* indices but were still significantly different from zero (Table 2). Both results suggest similar patterns in environmentally driven survival rates of these demersal and pelagic stocks.

Clustering of demersal stocks

Cluster analysis revealed several groups of demersal stocks within the BSAI ecosystem that showed similar patterns of variability in stock–recruit residuals (SR indices) over time (Fig. 6). We only show results from cluster analyses based on correlations among SR indices. Using correlations among log *R* series often resulted in different clusters that appeared to be driven by shared long-term trends in recruitment resulting from strong trends in spawning stock biomass. Because we were primarily interested in environmentally driven variability in survival rates, we chose to focus cluster analyses on patterns in SR indices, which better reflect those environmentally driven changes because the effect of changing spawner abundance has been removed.

Table 3. Pair-wise Pearson's correlation coefficients (r) between log(recruitment) (log *R*) or stock–recruit residuals (SR) of stocks of the same species from the GoA and BSAI, with p values in parentheses (adjusted for autocorrelation following Pyper and Peterman (1998)); significant correlations ($p < 0.05$) are in boldface type.

Species	log *R*	SR
Arrowtooth flounder	0.219 (0.472)	0.145 (0.578)
Flathead sole	–0.156 (0.499)	0.015 (0.961)
Walleye Pollock	0.141 (0.407)	–0.012 (0.948)
Pacific cod	**0.639 (0.014)**	**0.487 (0.021)**
Pacific ocean perch	**0.471 (0.042)**	**0.549 (0.018)**
Northern rockfish	0.338 (0.201)	0.493 (0.062)

At least three biologically sensible clusters were evident among Bering Sea groundfishes, including a gadid cluster (walleye pollock and Pacific cod), shelf flatfishes (arrowtooth flounder, yellowfin sole, rock sole, and flathead sole), and rockfishes (Pacific ocean perch and northern rockfish, which clustered together with Atka mackerel) (Fig. 6). In addition, Greenland turbot and Alaska plaice, in spite of large differences in life history and distribution, formed another cluster because both species showed a strong decrease in their SR indices in the late 1970s. All four clustering algorithms yielded the same clusters for Bering Sea SR indices. There was remarkable synchrony in the stock–recruit residuals of walleye pollock and Pacific cod in the Bering Sea but asynchrony between SR indices of the gadid group and those of the flatfish group (Fig. 6). This asynchrony in survival was evident in a number of negative correlations between the SR indices of the four flatfish species and those of Pacific cod or walleye pollock (average correlation $r = -0.33$). Averaging the species-specific SR indices across species within the gadid and flatfish clusters, respectively, confirmed the strong negative relationship between the two groups (correlation between combined SR series, $r = -0.65$, $p = 0.0008$).

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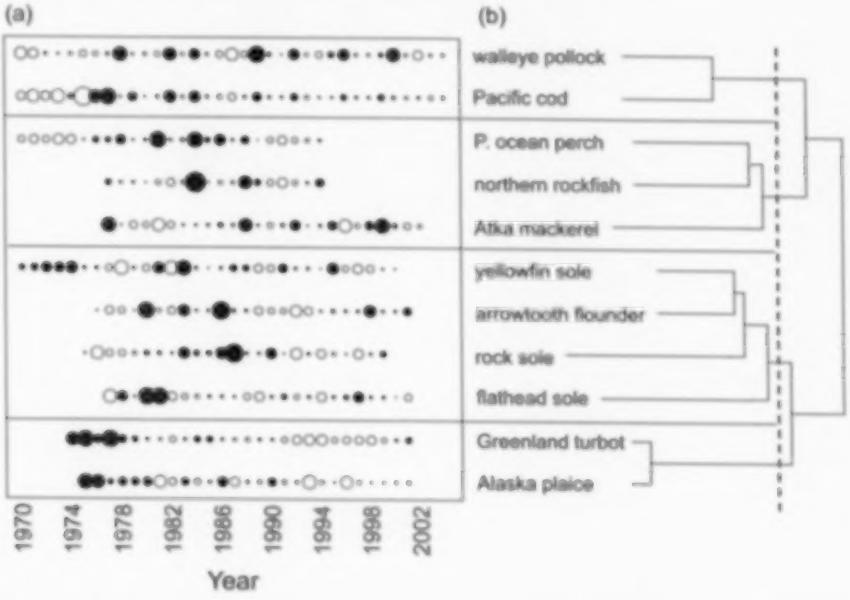
Fig. 6. (*a*) Time series of stock–recruit residuals (1970–2004 year classes, magnitude of SR indices reflected by diameter of circles; solid circles, positive residuals; open circles, negative residuals) and (*b*) cluster dendrograms based on group-average clustering of pairwise dissimilarities (based on Euclidean distances) among SR indices of 11 groundfish stocks in the Bering Sea – Aleutian Islands. The vertical broken line represents the chosen cutoff for identifying clusters. P., Pacific.



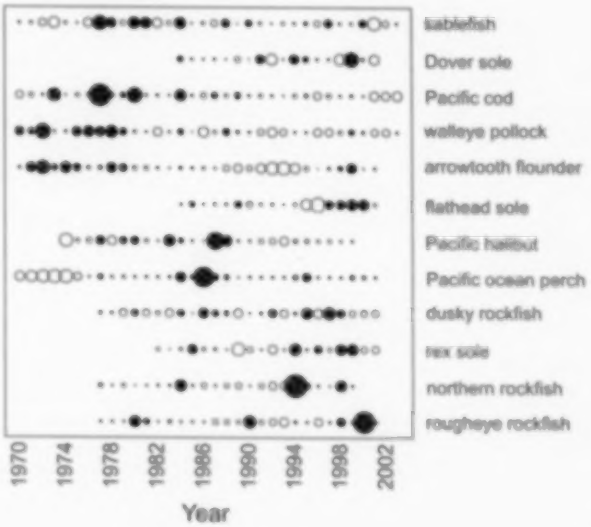
In the Gulf of Alaska we did not identify clear groupings among groundfish species (Fig. 7), and cluster composition was very sensitive to the clustering algorithm used. Only two pairs of species consistently clustered together because their SR indices were moderately positively correlated. These species pairs consisted of walleye pollock and arrowtooth flounder ($r = 0.55$, $p = 0.0008$) and Pacific ocean perch and dusky rockfish ($r = 0.43$, $p = 0.034$).

We examined the sensitivity of the clustering results to deleting the last two years of each time series because the more recent year classes are still poorly sampled owing to incomplete recruitment in many of the stocks. Clusters in the Bering Sea remained largely unchanged; however, northern rockfish SR indices (the shortest series with 16 years) no longer clustered with the rockfish group.

Combined indices of recruitment and survival rate

Combined indices of log R and stock–recruit residuals across 11 demersal stocks in the BSAI and across 12 demersal stocks in the GoA showed significant decadal-scale trends (Table 4), with typically above-average recruitment and survival rates in the 1980s and below-average recruitment and survival rates in the early 1970s and early 1990s (Fig. 8). The combined log R and SR series showed an increase from generally negative values in the late 1960s and early 1970s to mostly positive values in the late 1970s and 1980s. This increase corresponded to the well-known 1976–1977 climatic regime shift and was much less pronounced in the BSAI series. However, time series for individual demersal stocks in the BSAI were too short to adequately resolve a potential shift in the 1970s, and values of the combined indices are highly uncertain because they are based on

Fig. 7. Time series of stock–recruit residuals (1970–2004 year classes, magnitude of SR indices reflected by diameter of circles; solid circles, positive residuals; open circles, negative residuals) of 12 groundfish stocks in the Gulf of Alaska.



few stocks in early years. A shift from relatively high to low productivity occurred in the late 1980s to early 1990s and appeared to be more pronounced and longer-lasting in the Bering Sea than in the Gulf of Alaska, where demersal log R and SR indices increased substantially in 1994 and stayed

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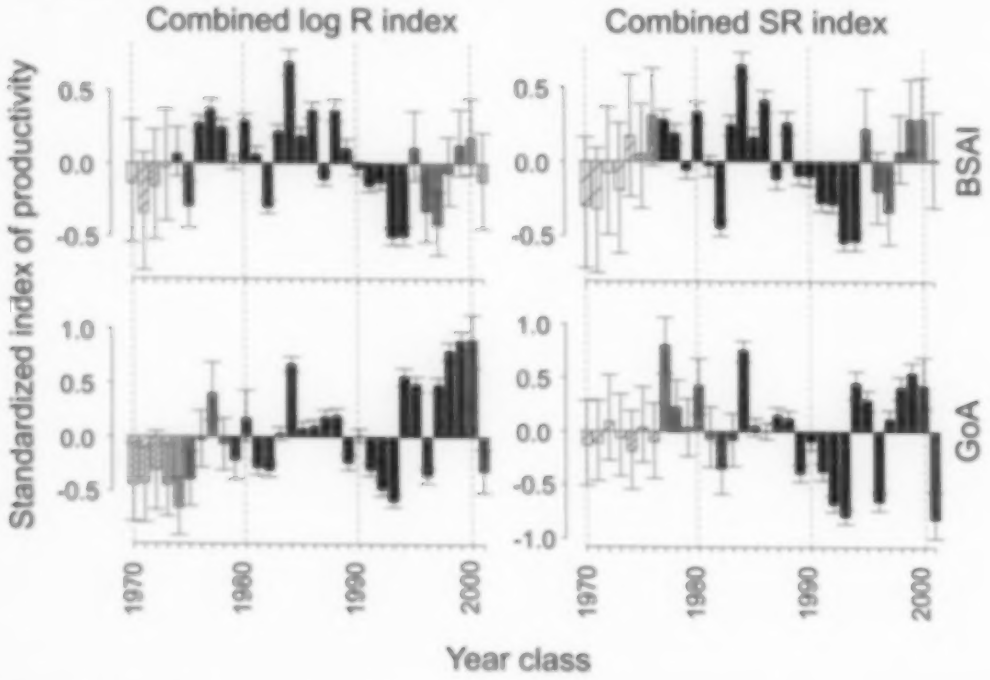
Table 4. Proportion of variability in combined productivity series (log recruitment (log *R*) or stock–recruit residuals (SR)) accounted for by decadal-scale trends (percent deviance explained in text) in the Bering Sea – Aleutian Islands (BSAI) and Gulf of Alaska (GoA).

	Percent deviance (*p* value)		Years of regime shifts	
Group	log *R*	SR	log *R*	SR
BSAI demersal	43.5 (**0.017**)	47.8 (**0.008**)	1976 (1991)	1976 (1991)
GoA demersal	43.7 (**0.017**)	21.1 (0.381)	1976, 1994	
BSAI pelagic	44.5 (**0.022**)	64.9 (**0.001**)	1977	1974
GoA pelagic	75.6 (**0.001**)	57.8 (**0.003**)	1977 (1986)	1974 (1986)

Note: Significant *p* values (boldface) refer to decadal-scale patterns relative to a constant mean model, based on an approximate χ^2 test. Years of regime shifts are significant change points ($p < 0.1$) in combined productivity series. Regime shifts were identified by the STARS method (Rodionov and Overland 2005). Years with significant decreases in log *R* or SR are indicated in parentheses, all other years reflect significant increases.

Fig. 8. Indices of log(recruitment) (combined log *R*, left column) and log(survival rate) (combined SR, right column) averaged across all groundfish stocks within the Bering Sea – Aleutian Islands (BSAI) and Gulf of Alaska (GoA). Solid bars represent years with data for all stocks, hatched bars represent years that do not have data for all stocks (lighter hatching corresponds to fewer years with data). Missing values were estimated by imputation, and error bars reflect the uncertainty (95% point-wise confidence interval) resulting from filling in missing values before averaging across stocks.



above average thereafter, with the exception of 1996 and 2001. However, as noted above, recruitment estimates for 2001 are highly uncertain.

Another notable feature of the combined demersal indices is that both log *R* and SR series show a marked increase from 1982, which had below-average anomalies in both ecosystems, to 1984, which had the largest positive anomaly of the entire time series in both cases (Fig. 8). This suggests that 1984 was an exceptionally productive year for demersal species in the these ecosystems, with 19 out of 23 species showing above-average recruitment (log *R*) and survival (SR) relative to the 1970–2001 averages. Although values of the indices in recent years are still highly uncertain, the numerous positive recruitment anomalies of Gulf of Alaska groundfish stocks after 1993 (Figs. 7, 8) provide some evidence that the low-productivity state of the early 1990s, in terms of recruitment and survival, gave way to higher productivity toward the end of the 1990s.

Pelagic stocks in both the Bering Sea and Gulf of Alaska showed a marked increase in recruitment and survival rates across stocks in the late 1970s corresponding to the 1976–1977 regime shift (Fig. 9). Unlike demersal stocks, pelagic stocks did not appear to respond to the documented 1988–1989 regime shift (Hare and Mantua 2000). Although the

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Fig. 9. Indices of log(recruitment) (log *R*, left column) and log(survival rate) (SR, right column) averaged across all pelagic stocks or stock groups (salmon + herring) within the Bering Sea – Aleutian Islands (BSAI) and Gulf of Alaska (GOA). Hatching and error bars as in Fig. 8.

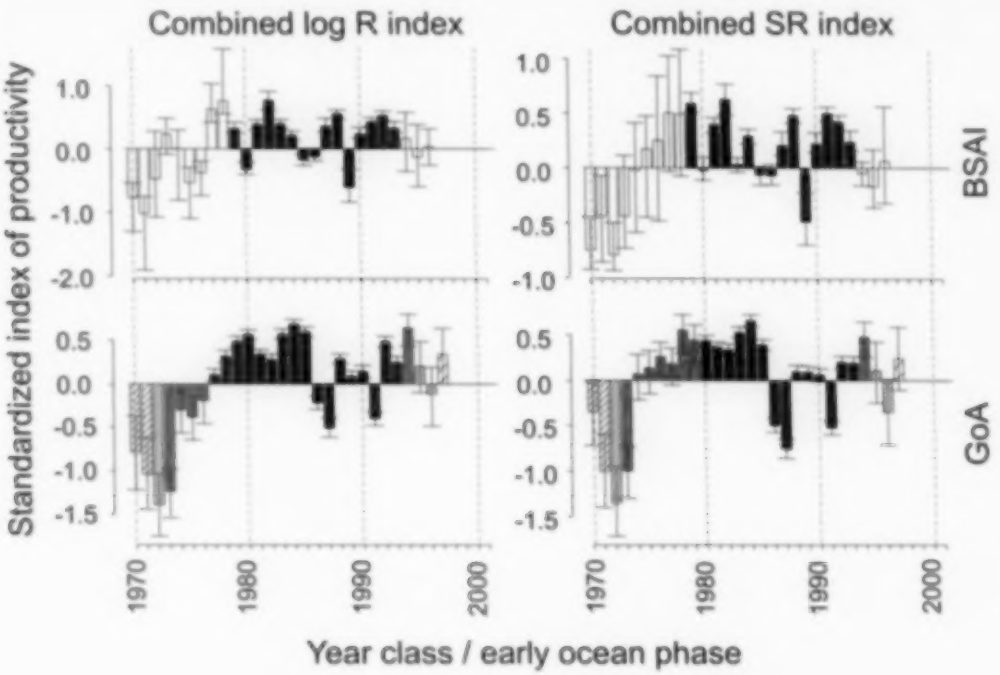

Table 5. Correlations (below diagonal) and corresponding *p* values (above diagonal) between combined indices of survival rates across all demersal stocks or pelagic stocks (primarily salmon) within a given ecosystem (BSAI, Bering Sea – Aleutian Islands; GoA, Gulf of Alaska).

		Demersal stocks		Pelagic stocks	
		BSAI	GoA	BSAI	GoA
Demersal stocks	BSAI		**0**	0.661	0.29
	GoA	**0.56**		0.94	0.37
Pelagic stocks	BSAI	0.11	0.015		**0**
	GoA	0.27	0.183	**0.571**	

Note: Significant correlations ($p < 0.05$) and corresponding *p* values are in boldface type.

combined log *R* and SR indices for the Bering Sea were below average in 1989, they were above average in the early 1990s. In the Gulf of Alaska, log *R* and SR indices showed a pronounced decrease between 1985 and 1986 but were generally above average again in the 1990s (Fig. 9).

Pair-wise correlations among the combined demersal indices suggest that overall demersal productivity displays similar patterns of variability in both the Bering Sea and Gulf of Alaska (Table 5). Similarly, combined indices of pelagic productivity are positively correlated between systems (Table 5). In contrast, there was no significant correlation between demersal and pelagic indices within a system or between the two systems (Table 5).

Change-point analysis

The change-point analysis identified apparent transition points (i.e., years when a major change occurred to a relatively persistent new "state") in the overall productivity of demersal and pelagic stocks in the Bering Sea and Gulf of Alaska based on an analysis of the combined productivity indices (log *R* and SR). We identified significant step increases ($p < 0.1$) in the combined log *R* and SR series for both ecosystems and for both pelagic and demersal species in 1976 or 1977 (Table 4). In addition, we found a significant step decrease in the combined log *R* index for BSAI demersal stocks in 1991, a significant step increase in the combined log *R* index for GoA demersal stocks in 1994, and a significant decrease in the combined indices for GoA pelagic stocks in 1986 (Table 4; Figs. 8, 9).

Significant change points for individual demersal stocks were detected throughout the available time series, with little evidence that these shifts corresponded to the known climatic regime shifts (Fig. 10). Average regime shift indices (RSI) from the STARS analysis, which average the estimated strength of shifts in a given year across all stocks with a significant shift in that year, showed no clear indication that abrupt shifts were concentrated in certain periods (Figs. 10*a*, 10*b*), although shifts in average log(recruitment) tended to occur more frequently in the late 1970s – early 1980s, as well as in the mid- to late 1990s. Shifts in recruitment or survival rates of pelagic stocks, in particular salmon, were frequently associated with the 1976–1977 climatic regime shift (Figs. 10*c*, 10*d*). Of 14 salmon stocks examined, eight showed a significant increase in log *R* and (or) SR in-

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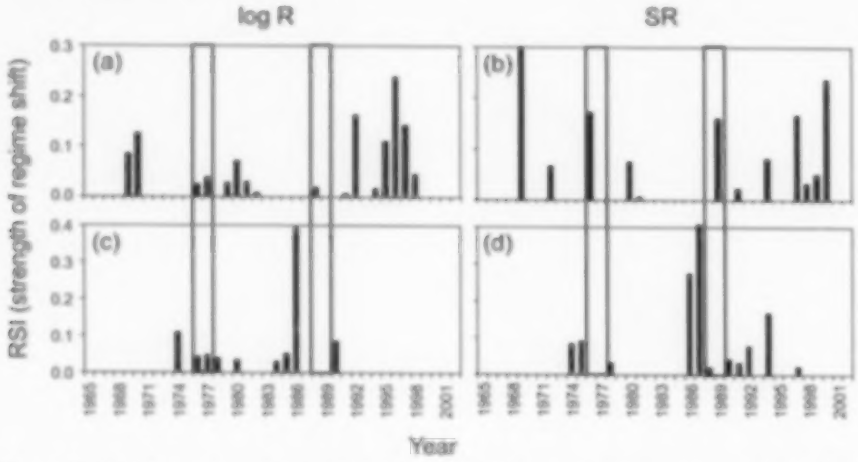
Fig. 10. Average regime shift indices (RSI) values (absolute values from the STARS analysis indicating strength of regime shift) for log(recruitment) indices (log *R*, left column) and stock–recruit residuals (SR, right column) by year across (*a*, *b*) 23 groundfish stocks and (*c*, *d*) 17 pelagic groups from the Gulf of Alaska and Bering Sea – Aleutian Islands. Vertical boxes indicate 1976–1977 and 1988–1989 regime shifts in climatic conditions.



dices between 1974 and 1980, whereas none showed a significant decrease. In contrast, shifts in the mid-1980s to mid-1990s were evenly divided between increases and decreases. Pronounced step decreases in the SR indices of two chum salmon stocks (central GoA and Prince William Sound) were observed in 1986 and 1987, respectively, resulting in a high regime shift index for pelagic stocks in these years (Figs. 10*c*, 10*d*). Results from the STARS analysis were not sensitive to eliminating the last two years from each series, although some of the shifts in the late 1990s were no longer significant when the last two years were eliminated.

Discussion

We examined variability in log *R* and stock–recruit residuals of pelagic and demersal fish stocks in two large marine ecosystems off Alaska. We assume that both log *R* and SR indices, at least in part, reflect real differences in productivity between years, although random variability due to uncertainties in estimation of spawner abundances and recruitment is likely to be substantial. Our SR indices, or residuals from each stock's best-fit stock–recruitment model, are preferable to abundance of recruits as indicators of productivity because they adjust for density-dependent effects of spawner abundance on productivity and are therefore more likely to reflect environmentally driven, or density-independent, components of variability (Peterman et al. 1998). However, recruitment may provide a better indicator of productivity in cases where the stock–recruitment relationship is highly uncertain and where fitting that relationship may introduce biases. Hence, we used both indices of productivity. Stock–recruit residuals, as well as recruitment, are also affected by predation; therefore, "environmental" effects on productivity include changes in abundance of important predators, regardless of whether these were caused by environmental variability, fishing, or other factors.

Within both ecosystems, we found significant between-species correlations for certain species groups that displayed similar patterns of variability at both interannual and decadal scales. Positive covariation among survival rate series of three species of salmon at spatial scales of up to about 1000 km has been documented previously (Pyper et al. 2005). Our results suggest similar covariation among certain groups of demersal species within ecosystems that have a spatial distribution across at least 1000–2000 km. Although different salmon species tend to show only positive covariation (Hare et al. 1999; Pyper et al. 2005), the demersal stocks examined here showed evidence of both positive and negative covariation, demonstrating that certain groups of species may be affected in opposite ways by shared environmental forcing. Most notably, both log *R* and stock–recruit residuals of flatfishes on the Bering Sea shelf were negatively correlated with those of gadids in the same region. This may be a consequence of environmental forcing that results in alternative pathways for production and favors pelagic feeders, such as pollock, during years with an early ice retreat but benthic-feeding flatfishes during years with a late ice retreat (Hunt and Stabeno 2002; Mueter et al. 2006).

Positive covariation in productivity indices of individual stocks and in the combined indices of overall productivity between the BSAI and GoA suggests that large-scale environmental influences affect the recruitment and survival of some species and overall productivity in both systems in similar ways. Likewise, positive covariation between the productivity indices for demersal and pelagic stocks within the GoA suggests that at least some of these stocks are affected in similar ways by environmental variability. In contrast, recruitment and survival rates of pelagic and demersal stocks within the BSAI appear to be determined by independent processes.

Much of the variability in recruitment and survival rates of some species and in overall productivity indices occurs at decadal time scales and suggests alternating periods of low and high productivity that correspond to the major oceanographic regime shifts observed in the Northeast Pacific (Hare and Mantua 2000). A large increase in salmon catches off

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Alaska was observed in the late 1970s (Hare and Francis 1995) and was consistent with increases in productivity as measured by the Ricker *a* parameter (Adkison et al. 1996; Peterman et al. 2003). The abundance of groundfishes also increased in the late 1970s in the GoA (Anderson and Piatt 1999) and in the BSAI (Conners et al. 2002), consistent with an increase in the recruitment of numerous demersal species following the 1976–1977 regime shift (Hollowed et al. 2001) and evident in unusually large values of our indices of overall productivity in 1977. In addition to previously observed increases in both pelagic and demersal productivity after the 1976–1977 regime shift in the GoA and BSAI, our results suggest a widespread decrease in recruitment and survival rates of demersal species in both ecosystems following the 1989 regime shift, with very low values in the early 1990s. A pronounced decrease in the recruitment of several flatfish species in the Bering Sea after 1988 was previously described by Wilderbuer et al. (2002), but poor recruitment in the early 1990s was also observed in Pacific Ocean perch and northern rockfish. The pronounced increase in the combined recruitment index for the GoA in 1994 reflects above-average recruitment and survival of most flatfish and rockfish species in the GoA from 1994 to at least 2000 but does not correspond to a known regime shift. Megrey et al. (2006) reported similar increases in model-based time series of zooplankton density and herring growth in the mid-1990s in the Northeast Pacific.

The response of individual groundfish stocks to the known major environmental regime shifts was highly variable, and there was little indication that observed shifts in recruitment or survival rates were unusually pronounced or had a higher frequency during the major regime shift periods. However, shifts that were detected during these periods were generally positive in the late 1970s and mostly negative in the late 1980s and early 1990s, resulting in relatively pronounced shifts in the aggregated indices of productivity. These patterns suggest that climatic regime shifts may affect overall fish productivity by altering the frequency of high survival or recruitment across stocks in a given year. This can result in periods with overall low or high productivity across stocks, in spite of large variability among stocks in their stock-specific responses.

Long-term trends or abrupt shifts and covariation in productivity among species have important implications for the assessment and management of fish stocks. Current models and projections generally assume that variability in recruitment arises from independent stochastic processes and recruitment is typically modeled as a function of spawning stock biomass plus random white noise (e.g., North Pacific Fishery Management Council 2005). To project future biomass levels, recruitments are usually drawn from the estimated, time-invariant stock–recruitment relationship or from recently observed recruitments. Given the changes in recruitment that we have found, it is clear that this approach tends to overestimate (or underestimate) future biomasses at the beginning of a low-productivity (or high-productivity) period. Therefore, management strategies need to be robust to both short-term and decadal-scale variations in recruitment.

Optimal management strategies depend on the nature of important sources of environmental variability, the ecology of the species of interest, and the management objectives (MacCall 2002). For a relatively short-lived species such as the sardine (*Sardinops sagax*), MacCall (2002) shows how harvest rates can be specified as a function of environmental conditions. Ideally, linking harvest policies directly to environmental variability should involve a clear understanding of the important effects of environmental factors on productivity, but that understanding is currently lacking for demersal species in the Northeast Pacific. Nevertheless, effects of regime shifts on productivity of some flatfish species in the BSAI have been estimated (for example, Wilderbuer et al. 2002) and have been incorporated into stock assessments by estimating separate stock–recruitment relationships for different regimes. However, a considerable postregime shift period (minimum of 10–15 years) is required to obtain reliable estimates of productivity for the new regime. Our results suggest that regime-like periods can be of relatively short duration and shifts may not be detected in time to incorporate their effects.

Another way to develop management strategies for fish species in regions with long-term trends or shifts in productivity is to use stock–recruitment models that assume one or more time-dependent parameters. Those parameters can be estimated annually using a Kalman filter to help track changes in productivity (e.g., Peterman et al. 2003). As long as the time lag is not too long between the environmental effects occurring and the estimate of its effect, then this method will improve management performance compared with the case in which the environment is constant or follows a white-noise pattern. Appropriate harvest policies for stocks with environmentally driven variability have also been explored under a variety of scenarios and indicate that either a constant harvest rate approach (Walters and Parma 1996) or variable harvest rate policies (Spencer 1997) can result in the best overall strategy. De Oliveira and Butterworth (2005) show that management actions can be improved by using environment-dependent stock–recruitment models, as long as these models explain about 50% or more of the total variation in recruitment. This is difficult to achieve given our current understanding, or lack thereof, of recruitment dynamics in most fish stocks.

Risks associated with the effects of environmental variability on individual stocks are magnified in the presence of covariation among stocks. Such covariation implies that a change in overall fish productivity affects the productivity of multiple stocks similarly and simultaneously, even if the effects may not be readily apparent at the stock-specific level but only at aggregate levels. Such effects are not explicitly accounted for by current single-species or multispecies models, but there are several ways in which covariation among stocks can be exploited to improve existing models. First, single-species models can take into account the effects of positive or negative covariation in productivity between species by including estimates for recruitment or survival rates of species that recruit at an early age as covariates in stock–recruitment models of species that recruit at later ages. For example, stock–recruit residuals of yellowfin sole and walleye pollock in the Bering Sea are strongly negatively correlated across year classes. Therefore, survival rate anomalies or stock–recruit residuals for a given walleye pollock

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year class, which can be reliably assessed at age 2, could be used to forecast yellowfin sole survival rates of the same year class, which recruits into the fishery several years later. The same approach may be applied to pink salmon, which recruit as 2-year-olds, and chum salmon, which have mainly 4- or 5-year-old recruits (Haeseker et al. 2005). Second, uncertainty in temporal trends in productivity and in the effects of environmental variability on productivity can be reduced by estimating trends and effects across covarying populations or species using appropriate multistock models such as mixed-effects or other hierarchical models (Mueter et al. 2002*a*). These improved estimates can then be incorporated into single-stock models as fixed effects or as prior distributions (Punt and Hilborn 1997). Third, multispecies assessment models could account for covariation among species by linking recruitment between species or modeling recruitment as a shared process with stock-specific variability.

In summary, this and other recent studies demonstrate that the recruitment and survival of different demersal and pelagic fish stocks in the Northeast Pacific does not fluctuate independently but shows significant positive or negative covariation. The covariation is strongest among certain demersal stocks sharing the same ecosystem, among salmon stocks of the same or different species sharing coastal marine areas during early ocean life, and among herring stocks that spawn within certain geographic regions. Limited spatial scales of covariation appear to result from regional environmental influences that affect survival rates of different species in similar or opposite ways (the latter for some demersal stocks). Although productivity of individual stocks primarily varies at interannual time scales, aggregate indices of overall demersal and pelagic productivity show strong decadal-scale patterns and stronger evidence of abrupt shifts such as those in the late 1970s and in the late 1980s – early 1990s. Such shifts imply changes in overall fish productivity that affect the probability and (or) magnitude of strong year classes across stocks. Rational management should account for changes in overall productivity, but methods to account for the effects of changing productivity are hampered by our ability to detect significant shifts in a timely manner. Nevertheless, the information inherent in the observed covariation among stocks can be exploited to potentially improve current single-species and multispecies models.

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PERSPECTIVE / PERSPECTIVE

Ecosystem-based fisheries management: some practical suggestions

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Abstract: Globally, there is increased scientific and public interest in the concept of ecosystem-based fisheries management (EBFM). This trend is fueled by a widespread perception that large-scale fishing operations are powerful forces altering the structure and function of marine ecosystems. It is acknowledged that management needs to better account for variations in ocean productivity, stock structure, and changing social values. Many countries are contemplating how to improve ocean fishery management. In the United States, fishery management bodies are experiencing pressure to undertake the daunting task of moving from their current single-species management plans to EBFM. Impediments include lack of a clear definition of EBFM, what it entails, or how to proceed. In this paper, characteristics of fishery management that are unique to EBFM are identified. The transition to EBFM needs to be evolutionary rather than revolutionary. A course of action is outlined that can be used to guide this transition. Modeling approaches and metrics useful for planning, implementing, and evaluating EBFM are discussed, with particular emphasis on management strategy evaluation.

Résumé : Il y a, à l'échelle globale, un intérêt croissant chez les scientifiques et le public en général pour le concept de gestion des pêches axée sur les écosystèmes (EBFM, ecosystem-based fisheries management). Cette tendance est alimentée par la perception que les opérations de pêche de grande envergure constituent des forces puissantes qui altèrent la structure et le fonctionnement des écosystèmes marins. On reconnaît que l'aménagement doit mieux tenir compte des variations de la productivité océanique, de la structure des stocks et des valeurs sociales changeantes. Plusieurs pays cherchent comment améliorer la gestion des pêches dans l'océan. Aux États-Unis, les organismes responsables de la gestion des pêches subissent de fortes pressions pour remplacer leurs plans actuels axés sur les espèces individuelles par l'EBFM. Une des difficultés est l'absence de définition claire de l'EBFM; il est aussi nécessaire d'en connaître les implications et de savoir comment procéder. Nous identifions ici les caractéristiques de la gestion des pêches qui se retrouvent exclusivement dans l'EBFM. La transition vers l'EBFM doit se faire par évolution plutôt que par révolution. Nous proposons un plan d'action pour guider cette transition. Nous discutons aussi des méthodologies de modélisation et des métriques utiles pour la planification, la mise en oeuvre et l'évaluation de l'EBFM avec une attention particulière portée à l'évaluation des stratégies de gestion.

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Introduction

The desire to move towards ecosystem-based fisheries management (EBFM) is a common theme in fisheries policy and management discussions worldwide. While EBFM means different things to different people, the underlying aim is ecologically sound resource conservation that responds to the reality of ecosystem processes. There is concern about the overexploitation of fishery resources that has occurred despite the declaration of 200 mile (1 mile = 1.609 km) Exclusive Economic Zones and the establishment of governmental institutions with fisheries management authority. Fisheries extraction is the anthropogenic effect most commonly invoked as an example of the forces altering the structure and function of marine ecosystems (Pauly et al. 2002; Essington et al. 2006). Consequently, increasing attention is being focused on changing fisheries management practices and principles to protect living marine resources on an ecosystem scale.

Historically, ecology, fisheries biology, oceanography, and fisheries economics have not been well integrated in fisheries management. It is generally acknowledged that far more attention needs to be focused on a coupled understanding of many factors for more successful fisheries management. Information on physical, chemical, and biological oceanography; population biology; ecological interactions of the various species of the fish community; and the likely social and economic ramifications of management changes must be considered explicitly. This integration should be carried out with a view to better management of resources on a sustainable basis (Charles 2001).

Many countries are contemplating how to implement modern ocean fisheries management concepts. The 13th International Council for the Exploration of the Sea (ICES) Dialogue Meeting (26–27 April 2004) discussed how ICES plans to introduce an ecosystem approach (Anonymous 2004*b*). As an outgrowth of this meeting, fisheries advice from ICES in 2004 was supplemented with ecosystem considerations dealing with both the impact of fisheries on the ecosystem and the impact of ecosystems on fisheries (Anonymous 2006*b*). In 2005, ICES began discussions on reforming the structure of its expert groups that deliver science and advice, and a special meeting took place in March 2006 to develop a blueprint for the new science and advisory structures that will be required within ICES to service the demands of the ecosystem approach (Anonymous 2006*b*). The Australian Fisheries Management Authority has set out to assess the risks that fishing poses to the ecological sustainability of the marine environment for major Commonwealth fisheries (Anonymous 2006*a*). Ecological risk assessments are considered to be a key component of EBFM by the Australian Fisheries Management Authority. In 2002, Canada issued the "… Policy and Operational Framework for Integrated Management of Estuarine, Coastal and Marine Environments", which provided conceptual guidance on integrated management and planning (Anonymous 2005). This policy, which includes the concept of an ecosystem-based approach, is being tested for the Eastern Scotian Shelf (Anonymous 2004*c*). Echoing concerns contained in reports and studies regarding the sustainability of marine ecosystems and the depletion of many fish species, the US Commission on Ocean Policy (Anonymous 2004*a*) recently recommended that the United States move towards EBFM. Despite all the interest, substantial operational and definitional issues remain with EBFM and how it might be implemented.

Within the United States, Fishery Management Councils (FMCs), established in the mid-1970s under the authority of the Magnuson–Stevens Fishery Conservation and Management Act (Magnuson–Stevens Act), are the rule-making bodies charged with developing federal fishery management (consistent with other applicable policy). FMCs are faced with growing national momentum to adopt EBFM. Congressional reauthorization of the Magnuson–Stevens Act includes provisions to help redirect fishery management policies and procedures away from the traditional emphasis on single-target species and towards EBFM. Many of the FMCs' management actions can arguably be considered to reflect an overall ecosystem philosophy (Witherell 2004), and some Magnuson–Stevens Act provisions have already led to protection of essential fish habitat (EFH), reduction of bycatch, and rebuilding of overfished stocks. However, attempts at making these concepts operational based on clearly specified ecosystem guidelines and standards are still in an early stage.

There have been numerous reviews, workshops, and conferences that have addressed what EBFM is and how it should be implemented (NMFS 1999; NRC 1999; Witherell 2004). This review (initiated at the request of the Pacific States Marine Fish Commission) addresses three practical issues related to EBFM: (*i*) How should EBFM be defined for use by FMCs and other regulatory bodies? (*ii*) What characteristics are specific to an EBFM approach? (*iii*) What are the next steps that FMCs and other regulatory bodies should take to move forward from the existing management approaches to a management system that would, over time, explicitly incorporate EBFM considerations into fishery assessment and management?

While the discussion that follows draws extensively from experience in the United States, it is believed that the guidance provided will be relevant worldwide to most parties and agencies responsible for the management of fisheries.

Defining EBFM

At present, the dominant fishery management paradigm focuses on individual species and does not incorporate ecosystem considerations in a comprehensive and transparent way. The shortcomings of this paradigm have been recognized, but not yet fully corrected (Mangel et al. 2002). Many definitions of an ecosystem-based approach to natural resource and fisheries management have recurring themes (Table 1). There is recognition of a broader constituency of uses and users of the marine environment (including fishing) and the need to accommodate and reconcile the many goals of these users so that future generations can also benefit from the full range of ecosystem goods and services. There is recognition that humans are an essential component of the ecosystem in which fishing takes place. Most importantly, these definitions recognize the interactions among physical, biological, and human components within the system. Therefore, it can be concluded that the purpose of an EBFM approach is to plan, develop, and manage fisheries in a

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Table 1. Some existing definitions of an ecosystem-based approach to management (or fisheries management).

The North Pacific Fishery Management Council (Witherell et al. 2000)

An ecosystem-based approach to fisheries management is defined as the regulation of human activity towards maintaining long-term system sustainability (within the range of natural variability as we understand it) of the North Pacific covering the Gulf of Alaska, the Eastern and Western Bering Sea, and the Aleutian Islands region.

The Food and Agricultural Organization of the United Nations (FAO Fisheries Department 2003)

An ecosystem approach to fisheries strives to balance diverse societal objectives by taking into account the knowledge and uncertainties about biotic, abiotic, and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries.

The Scientific Consensus Statement on Marine Ecosystem-Based Management (McLeod et al. 2005)

Ecosystem-based management is an integrated approach to management that considers the entire ecosystem, including humans. The goal of ecosystem-based management is to maintain an ecosystem in a healthy, productive, and resilient condition so that it can provide the services humans want and need. Ecosystem-based management differs from current approaches that usually focus on a single species, sector, activity or concern; it considers cumulative impacts of different sectors.

The National Research Council (NRC 1999)

Ecosystem-based management is an approach that takes major ecosystem components and services — both structural and functional — into account in managing fisheries. It values habitat, embraces a multispecies perspective, and is committed to understanding ecosystem processes. Its goal is to achieve sustainability by appropriate fishery management.

National Oceanic and Atmospheric Administration (Murawski and Matlock 2006)

An ecosystem approach to management (EAM) is one that provides a comprehensive framework for living resource decision-making. In contrast to individual species or single-issue management, EAM considers a wider range of relevant ecological, environmental, and human factors bearing on societal choices regarding resource use.

manner that addresses the multiple needs and desires of society without jeopardizing the options for future generations to benefit from the full range of ecosystem goods and services.

The authors propose the following as a definition of EBFM: "Ecosystem-based fishery management recognizes the physical, biological, economic, and social interactions among the affected components of the ecosystem and attempts to manage fisheries to achieve a stipulated spectrum of societal goals, some of which may be in competition."

Characteristics of EFBM

The identification of characteristics of EBFM is facilitated by recognizing its aim as defined above. Numerous lists of characteristics or elements have been proposed by, for example, the Ecosystem Principles Advisory Panel (NMFS 1999), the Scientific Consensus Statement on Marine Ecosystem-Based Management (McLeod et al. 2005), and the Marine Fisheries Advisory Committee's Ecosystem Approach Task Force (Busch et al. 2003). Table 2 (taken from McLeod et al. 2005) represents a good starting point for characterizing EBFM as proposed heretofore, but the authors believe that additional factors are also important. The following seven elements are specific to EBFM and are distinct from those considered routinely in single-species approaches to fisheries management. (1) Ensure that broader societal goals are taken into account. (2) Employ spatial representation. (3) Recognize the importance of climatic–oceanic conditions. (4) Emphasize food web interactions and pursue ecosystem modeling and research. (5) Incorporate improved habitat information (target and nontarget species). (6) Expand monitoring. (7) Acknowledge and respond to higher levels of uncertainty. These should, therefore, be the focus for changes to current approaches. The following sections outline each of these elements further.

Broader goal specification and recognition

EBFM acknowledges differing uses of an ecosystem and its resources. Since fisheries goals are only a subset of societal goals, EBFM needs to embrace a broader set of impacts and goals. In the United States, this may require expanded participation and representation in the FMC process. Pertinent societal goals should include national, regional, and fishery-specific goals, but also would extend beyond conventional fisheries goals. In the United States, goals are based to a greater or lesser degree upon the Magnuson–Stevens Act, the Endangered Species Act, and the Marine Mammal Protection Act. Within an EBFM approach, broader goals reflecting society's changing values for ecosystem products and services will need to be accommodated more explicitly in management models and actions, for example as embodied in the Marine Sanctuaries Act. However, moving from high-level policy goals to operational goals remains a major challenge in situations where the goals are broad concepts such as "ecosystem integrity", "ecosystem health", and "biodiversity" (Sainsbury et al. 2000). Given a broader stakeholder base under EBFM, there also will be a need for institutions to coordinate consultations. Joint decision-making will be needed between fisheries and other non-fishery-related user groups that operate and interact in the same geographic area. Initial steps in this direction have been taken by some FMCs, as they broaden representation of civic and environmental groups on advisory committees.

Spatial representation

Accounting more explicitly for space (spatial thinking) is a practical way of moving forward with EBFM. Although accounting for space is fundamental to an understanding of

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Table 2. Characteristics of an ecosystem-based approach to fisheries management identified. (From McLeod et al. 2005, reproduced with permission of Communication Partnership for Science and the Sea (COMPASS).)

1. Make protecting and restoring marine ecosystems and all their services the primary focus, even above short-term economic or social goals for single services.
2. Consider cumulative effects of different activities on the diversity and interactions of species.
3. Facilitate connectivity among and within marine ecosystems by accounting for the import and export of larvae, nutrients, and food.
4. Incorporate measures that acknowledge the inherent uncertainties in ecosystem-based management and account for dynamic changes in ecosystems. In general, levels of precaution should be proportional to the amount of information available; the less that is known about a system, the more precautionary management decisions should be.
5. Create complementary and coordinated policies at global, international, national, regional, and local scales, including between coasts and watersheds (appropriate scales for management will be goal-specific).
6. Maintain historical levels of native biodiversity in ecosystems to provide resilience to both natural and human-induced changes.
7. Require evidence that an action will not cause undue harm to ecosystem functioning before allowing that action to proceed.
8. Develop multiple indicators to measure the status of ecosystem functioning, service provision, and effectiveness of management efforts.
9. Involve all stakeholders through participatory governance that accounts for both local interests and those of the wider public.

population dynamics processes (e.g., fish movements over time and space) and stock structure, single-species management has tended to focus more on temporal and age-structured considerations. Spatial thinking can help define how and where human activity (both fishing and nonfishing) affects the ecosystem, and spatial management can help to resolve conflicts among user groups through zoning for different uses, including nonextractive uses (the latter, for example, through the implementation of a system of no-take Marine Protected Areas). Without an explicit consideration of space when making management decisions, species are managed as homogeneous populations, which may impede the ability to develop prudent management measures, such as spreading catch out spatially and temporally to protect life-history characteristics and biodiversity. Spatial considerations are already being accounted for to some extent when fishery management decisions are made in the United States. For example, (*i*) restrictions were placed on the eastern Bering Sea and Gulf of Alaska walleye pollock (*Theragra chalcogramma*) fisheries to protect local availability of prey for Steller sea lions (*Eumetopeus jubatus*) around haul-out and breeding locations; (*ii*) salmon fisheries on the west coast of the United States are managed both spatially and temporally to maintain a complex stock structure and to allocate benefits between coastal communities and user groups (PFMC 2006*a*); and (*iii*) west coast groundfish management has included extensive spatial closures to reduce bycatch of overfished stocks and to protect EFH (PFMC 2006*b*).

Although a wide variety of spatial models have been developed (Quinn and Deriso 1999), there has been limited application of these models in fisheries because of the lack of necessary data on fish movement and spatial variation in biological parameters. Even when movement data are available, (e.g., Pacific halibut (*Hippoglossus stenolepis*), Quinn et al. 1990; and Gulf of Alaska sablefish (*Anoplopoma fimbria*), Heifetz and Quinn 1998), spatial models are rarely used as the basis of stock assessments, because of their greater complexity. Exceptions to this are the assessment of hoki (*Macruronus novaezelandiae*) off New Zealand (Francis 2004) and sharks off southern Australia (Punt et al. 2005). Integral to the move to EBFM is the routine examination in stock assessments of the evidence for stock and spatial structure. The lack of evidence for spatial structuring owing simply to lack of data should not be a reason to ignore the possibility of such structure. Moreover, in many cases, reasonable recommendations regarding how harvests should be distributed spatially can be made using data from surveys and catch information if there is evidence for spatial structuring, but there are insufficient data to conduct stock assessments that are spatially structured. For example, survey and catch information is already used to distribute catches spatially for many of the stocks managed by the North Pacific Fishery Management Council (NPFMC) (e.g., Gulf of Alaska walleye pollock, Pacific cod (*Gadus marcocephalus*), and sablefish; Heifetz et al. 1997).

The increasing application of geographic information systems (GIS) can be combined with traditional tagging techniques, more recent methodologies such as highly variable genetic markers (Hankin et al. 2005), and otolith microchemistry (Campana and Thorrold 2001; Miller et al. 2005; Barnett-Johnson et al. 2006) to identify population structure and estimate the extent of mixing and migration for a species. Such combined approaches will also facilitate taking better account of the spatial considerations in management.

Climatic–oceanic conditions

There is ample evidence of the importance of regime shifts in climate and interannual variation in oceanographic conditions on the growth, reproduction, and survival of fish and other marine species (Logerwell et al. 2003; King et al. 2005; Wells et al. 2006). Some regimes favor some species over others, and this depends on life-history characteristics (e.g., longevity and maturity schedules), their position in the food chain, and other factors. For example, it is known that salmon, sardines, marine mammals, Alaska crab, walleye pollock, and other groundfish species on the west coast of the United States are sensitive to regime changes (Beamish 1995; McGinn 2002). In this respect, the difference between the North Pacific and US west coast in the last 30 years is instructive. The North Pacific (the Gulf of Alaska and the Bering Sea) experienced good environmental conditions for fish productivity beginning in about 1976. In contrast, Washington, Oregon, and California experienced poor environmental conditions over the same period (Hare et al. 1999; Peterson and Schwing 2003; King et al. 2005). As a result,

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fisheries in the North Pacific have been extremely productive, while those on the west coast have suffered. The poor environmental conditions off the west coast contributed to some extent to the decline of many of the groundfish species off the west coast (although fishing was almost certainly the main cause) and therefore have contributed to the need for the stringent management measures that have been implemented in this area (PFMC 2004).

Calculations of maximum sustainable yield and the rate at which overfished species are likely to rebuild are generally based on data for a period of years where it assumed that productivity was constant and will continue to be so for the projected future (Punt and Methot 2005). It therefore would be prudent for management strategies to respond to the possibility of climate changes that alter population or ecosystem productivity to detect climate-regime-related changes as soon as possible and to develop indicators to anticipate them. Necessarily, the information on how climatic–oceanic patterns might impact fish species has been obtained from retrospective analyses of oceanographic conditions and is seldom used for projection. Nevertheless, while predictive capability is still low, an important part of EBFM is to identify management strategies that are robust to ocean climate factors and their effects on species' life histories. However, it may someday be possible to develop fisheries management processes that can respond rapidly, when changes are initially detected, if ongoing efforts to expand ocean observation systems are successful. Further research to understand how ocean climate affects ecosystem processes will help in this process (Field et al. 2006) as will research into which factors provide the earliest indication of a change in the productivity regime.

Food web interactions

Food web considerations are important in EBFM. For example, there have long been indications that harvesting species low on the food chain has disproportionately larger impacts on species at the top of the food chain. Similarly, there are indications that selective harvest of desirable top predator species can lead to simplified community structure and redirection of fisheries toward lower and lower trophic levels (Pauly et al. 2002; Essington et al. 2006).

Collection and analysis of fish stomachs to determine prey consumption by predators is crucial for the development of the information base to model and understand food web interactions. As foraging theory predicts, many species are opportunistic in their feeding habits within trophic categories (e.g., piscivores, benthic carnivores, etc.) and will switch prey if presented with appropriate-sized prey and encounter opportunity. Information on diets and how diets change over time within trophic categories is necessary to develop adequate trophic ecosystem models. Unfortunately, with the exception of databases maintained by the NMFS Northeast Fishery Science Center for the northwest Atlantic and by the Alaska Fisheries Science Center for the Gulf of Alaska and eastern Bering Sea, there are no comprehensive, long-term databases in the United States upon which reliable ecosystem models could be based.

Information on diet composition is, however, not sufficient to quantify the functional relationships between predators and prey. Changes in ocean climate can cause temporal changes in predator and prey distributions that in turn lead to changes in trophodynamics. For example, Humboldt squid (*Dosidicus gigas*) have recently extended their northern range along the west coast of the United States. Top predators such as seabirds may not be able to switch prey quickly when their preferred prey species is depleted. The impact of the loss of forage species is then evidenced by increased seabird mortality (Ainley et al. 1995; Sydeman et al. 2001).

The predictions from ecosystem models can be sensitive to assumptions regarding the functional relationships determining predation. As a result, the ability to quantify and predict how natural mortality of fish and other organisms changes over time and space is currently limited. This leads to increased uncertainty and the need for precautionary management. Some management jurisdictions (e.g., the NPFMC; Anonymous 1998*a*) have responded to this uncertainty by banning or severely restricting harvests of forage fish (Constable and de la Mare 1994; Butterworth and Punt 2003). Unlike the current generation of single-species models, most ecosystem models as presently implemented do not adequately treat uncertainty (International Whaling Commission 2004). However, even if interactions are poorly quantified, ecosystem models can be used to help shift focus to ecosystem thinking.

The implications of trophodynamic changes for fisheries management will become clearer as models are refined and species interactions are better understood. The current generation of ecosystem models should therefore be modified to more explicitly treat uncertainty. Once modified, they should be used to evaluate the benefits of additional field research and to identify the most critical data gaps. Ecosystem modeling for management support should be more focused on quantifying trade-offs among diverse goals.

It is necessary to identify the data that are cheap or easy to collect (e.g., remote sensing data collected by others), as well as to set priorities for the most important information that may be expensive to collect, but that would provide insight into important ecosystem processes. For example, there is a need to collect ecosystem data that are not associated with data already collected during fishing activities, since fishery operations are frequently limited in space and time. Further, it is important to continue research on how climatic–oceanic patterns impact target and nontarget species.

Habitat

An increased and expanded focus on habitat considerations is needed for EBFM. The Magnuson–Stevens Act calls for the protection of EFH from fishing impacts to the extent that practical, current understanding of physical habitat for spawning, rearing, feeding, etc. of fishery species is limited. However, existing knowledge of ephemeral pelagic habitat (e.g., oceanographic features like fronts, eddies, and current patterns) is even more rudimentary (Grimes and Kingsford 1996; Grimes 2001; De Robertis et al. 2005). Similarly, habitat is an important consideration for protected species and for nonmanaged species, but habitat needs are understood for only a small fraction of these species. There

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also is a need to focus more attention on understanding cumulative effects from both fishing and nonfishing (e.g., point and nonpoint pollution, industrial development, and habitat alteration) activities on habitat and how productivity of both the target and nontarget species is affected.

Expanded scope of monitoring and research

Monitoring and research for EBFM will be qualitatively new, in that it will involve new and different subject matter, but it will not replace the need for continuing current monitoring activities such as fishery-independent surveys to monitor target species. EBFM monitoring and research will be more focused on achieving a quantitative understanding of biological interactions. At an immediate and practical level, EBFM will require monitoring of total fishery removals for both target and nontarget species. There will also be a need to understand the cumulative effects of anthropogenic impacts on productivity, including those from nonfishing activities. In addition, monitoring is essential to determine the magnitude and timing of ocean climate changes and to understand how changes affect various target and nontarget species. The evaluation and improvement of marine ecosystem models should receive high priority, although the initial focus of this work should be on quantifying uncertainty and identifying critical data needs. Ecosystem modeling also needs to be more focused on quantifying trade-offs among diverse goals.

Acknowledge and respond to high levels of uncertainty

High levels of uncertainty are a prominent feature of the present scientific understanding of ecosystem functioning, interactions among ecosystem components, and feedback loops within the ecosystem. Furthermore, the present generation of marine ecosystem models is rudimentary. Therefore, the harvest decision rules used by the FMCs to determine catch limits need to evolve in the direction of incorporating explicit probabilities (e.g., as is already the case for the decision rule used by the International Whaling Commission (1999) for the management of commercial whaling) to cope systematically with the high level of uncertainty. This will also require an evolution of policy guidelines to include a quantitative standard for what is adequately precautionary.

Implementation of EBFM

EBFM is neither inconsistent with nor a replacement for current fisheries management. This means that EBFM should be adopted as an incremental extension of current fisheries management approaches. The challenge is to find ways to move forward given the potential costs imposed by the probable decreased harvests and the high degree of uncertainty likely to be associated with EBFM and not allowing the costs and uncertainty to be a license to maintain the status quo. Rather, the uncertainty should be taken as a mandate to improve current understanding.

The single-species assessment and management approach has a long empirical record, with well-defined models (Quinn and Deriso 1999), and research is being conducted to fill data gaps to further improve these models (Quinn 2003; Quinn and Collie 2005). Properly used, the single-species approach has been effective. Outright failures have not, for the most part, been due to the science and management approach, but rather have been due to data limitations and the lack of political will (Fogarty and Murawski 1998; Sissenwine and Mace 2001).

The single-species approach does incorporate some ecosystem considerations at least implicitly or indirectly. For example, some of the emergent properties of ecosystems can be captured, at least retrospectively, in assessment models by allowing weight-at-age to change over time and by estimating annual recruitments. However, the ecosystem is generally treated as a single, collapsed background factor in these models. Other examples where ecosystem features have been included in single-species stock assessments and management decisions are (*i*) a stock–recruitment curve with density dependence for the target species that arises from predation by another species (Quinn and Deriso 1999); (*ii*) modeled, time-varying, natural mortality that may be due to predation or disease effects (Fu and Quinn 2000; Marty et al. 2003); (*iii*) a set of years used to define biological reference points that takes into account perceived regime shifts (Quinn and Collie 2005); and (*iv*) management that accounts for stocks with low productivity by restricting harvest on all species to avoid bycatch of overfished or protected species (PFMC 2004; Breen et al. 2003). Such "weak stock" management recently restricted commercial Chinook salmon (*Oncorhychus tshawytscha*) fishing along most of the US west coast to protect the endangered Klamath River fall Chinook salmon (PFMC 2006*c*).

Perhaps the most important change required for EBFM is the change to a set of goals beyond those associated with harvest of targeted fish species. Additional scientific inputs will be needed to construct models that accommodate broader goals and alternative management strategies. As noted by Goodman et al. (2002), "… Moving from the conventional assessment view towards an ecosystem view involves a shift in the components of fundamental underlying ecological science that is relied upon. In essence, for current fishery management, population ecology is the fundamental ecological science, but for an approach that takes ecological and ecosystem considerations into account, community ecology is the fundamental ecological science. For example, when one thinks about single species, there can be "excess production" from a stock, but when one thinks about the "needs" of all the other species in an ecosystem, the notion of excess production from a single member of the community becomes far more complicated."

To be practical, the move to EBFM must be evolutionary rather than revolutionary. According to Goodman et al. (2002), the evolution involves three stages. In the first stage, assessments focus on the status of the target species and its predators and prey. Assessments are broadened in the second stage to (*i*) take into account environmental effects in a more direct fashion when determining the status of the target species and (*ii*) incorporate measures for the direct effects of fishing activities other than those on the target species (e.g., bycatch, incidental mortality, and effects on habitat). In stage three, the environment, target stock, and its predators and prey are integrated explicitly into an assessment before catch limits and other management measures are selected.

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Table 3. Actions to promote ecosystem-based fisheries management (NMFS 1999).

1. Delineate the geographic extent of the ecosystem(s) that occur(s) within FMC (Fishery Management Council) authority, including characterization of the biological, chemical, and physical dynamics of those ecosystems, and "zone" the area for alternative uses.
2. Develop a conceptual model of the food web.
3. Describe the habitat needs of different life-history stages for all plants and animals that represent the significant food web and how they are considered in conservation and management measures.
4. Calculate total removals — including incidental mortality — and show how they relate to standing biomass, production, optimum yields, natural mortality, and trophic structure.
5. Assess how uncertainty is characterized and what kinds of buffers against uncertainty are included in conservation and management actions.
6. Develop indices of ecosystem health as targets for management.
7. Describe available long-term monitoring data and how they will be used.
8. Assess the ecological, human, and institutional elements of the ecosystem that most substantially affect fisheries and are outside FMC – Department of Commerce authority. Included should be a strategy to address those influences to achieve both Fishery Management Plan and Fishery Ecosystem Plan objectives.

The second and third stages both recognize the existence of ecosystem interactions. The second stage differs from the third in that it does not attempt to quantify the surplus production that must be reserved to satisfy ecosystem needs, nor does it attempt to modify fishing behavior to specifically mitigate adverse impacts other than those on the target species. The focus of the second stage is on the determination of the status of target and nontarget species and the evaluation of measures for the more tractable problems, such as EFH and bycatch.

In moving to EBFM, the challenge will be to diagnose the respective influences of individual environmental and ecological factors (e.g., climate and oceanographic conditions) and to develop an understanding of important processes and interactions. High levels of uncertainty will be associated with the representation of these relationships. The uncertainty results from the limitations of currently available data for estimating parameters for ecosystem models, for validating these models, and for understanding critical processes and the inherent limits of predictability of some of the underlying biological and oceanographic processes.

A critical danger is that without any track record for such models, the assumptions could be completely wrong. For this reason, changes to management strategies should also be evolutionary. During the transition to EFBM, management strategies should be similar to those used at present, (e.g., based primarily on conservative single-species management). However, selection of new management strategies that are more robust to uncertainty is possible when the results of several different ecosystem models are consistent and a management strategy evaluation shows good performance across the spectrum of possibilities. In other words, there are technical means for filtering out the most risky aspects of new, unproven models, while still being innovative.

The management system may look similar to that used at present during the transition to EBFM. However, the increased importance and use of ecosystem models will assist in the identification of approaches to consider when selecting the technical basis for providing assessments, selecting the decision rules that use the results from the assessments to define management measures, and planning investments in research and monitoring. The design and use of new models also should assure that there is at least qualitative consideration of interactions before management decisions are made.

NMFS (1999) provided a list of actions that could be taken to promote EBFM (Table 3). While the information associated with the eight items in Table 3 is relevant, it is not clear how practical they are. The concepts contained in Table 3 can be modified and extended to provide more implementation-related detail. The authors' proposed modifications are organized around application of the management strategy evaluation (MSE) approach (Goodman et al. 2002). MSE assesses the performance of a range of management strategies against a set of management goals and allows comparisons of performance among the different strategies. MSE evaluates how sensitive management strategies are to uncertainty (e.g., climate, spatial distribution, and sampling effectiveness) and may be used to evaluate a decision process that has already been adopted. Management strategies, as evaluated using the MSE approach, need to be fully specified, including, for example, specification of the data that are to be collected to support decision-making, how those data are to be analyzed to provide the input to any decision rules, and the decision rules themselves. The outcomes of an MSE are predictions of the expected performance, the trade-offs among the various (usually conflicting) management goals, and the sensitivity of the outcomes of the management strategies to various sources of uncertainty. The process of conducting an MSE to achieve EBFM involves several steps. Though the level of information and data available will change over time, the considerations identified will apply in both the short and long term.

The authors' modified list of actions is as follows: (1) Delineate and characterize the ecosystem including the ecological, human, and institutional elements of the ecosystem that most substantially affect fisheries. (2) Determine and quantify management objectives that reflect societal goals (e.g., in a single-species context, one of goals of the PFMC for groundfish is to minimize the probability that any stock is depleted to below the overfished level of 25% of the unfished biomass; however, ecosystem goals related, for example, to quantitative representations of the metrics identified by Murawski (2000) also need to be defined). (3) Develop conceptual models of (*a*) the food web and (*b*) the influence

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of oceanographic and climatic factors. (4) Describe the habitat needs of different life-history stages of plants and animals that represent the "significant food web" and how they are considered in conservation and management measures. (5) Expand and modify the conceptual model of the ecosystem to include life-history characteristics and spatial variation. (6) Calculate total removals, including incidental mortality, and show how they relate to standing biomass, production, optimum yields, natural mortality, and trophic structure. (7) Construct a range of alternative system models (often referred to as operating models) based on the conceptual models. Ideally, the range of system models (and the values for their parameters) should be sufficiently broad so that all plausible hypotheses regarding ecosystem processes are represented. Existing data will be used to estimate some of the parameters of these models, while for parameters that are poorly determined by existing data sensitivity will need to be explored until additional data are collected. (8) Identify a set of candidate management strategies. This will involve (*a*) assessing how uncertainty is characterized by the management agency and what kinds of buffers against uncertainty are included in conservation and management actions; (*b*) developing indices or indicators of ecosystem health as targets for management, including those based on models and how these indices can be used as the basis for decision-making. "Traffic light" approaches may be useful (Caddy 2002). Traffic light approaches assemble suites of environmental, biological, and socio-economic data into matrices of colored indicators across time. Examples for the Bering Sea and Gulf of Alaska ecosystems are given in Boldt (2006). Some have proposed using these indicators as "stop" or "go" recommendations for management. For example, if forage fish density falls below a set level, then fishing mortality would be reduced. (*c*) Describing long-term monitoring that is expected to continue and define how these data will be used for updating the parameter estimates used in the decision rules. (9) Use the management strategies to manage the simulated ecosystems represented by the system models and keep score of the achieved performance as defined by the management objectives. (10) Use the results of the simulations to (*a*) identify robust management strategies, critical data gaps, and ecological processes and (*b*) put plans in place to address the critical data gaps. (11) Select from among management strategies in light of their calculated performance and implement the selected management strategy. (12) Monitor to verify success of the management strategy and the validity of the system model on which its selection was based. (13) Revise the set of system models (hopefully the monitoring will have shown that some of the original system models were more plausible than others) and the management strategy (based on discrepancies between actual and target harvest outcomes based on the monitoring data).

Clearly the current portfolio of implemented ecosystem models does not yet span the full range of plausible system models. However, substantial progress towards implementing EBFM can take place if attempts are made to follow each of the above steps. Specifically, several ecosystem models have been developed for the US west coast, the Gulf of Alaska, and the Bering Sea – Aleutian Islands regions (Livingston and Methot 1998; Jurando-Molina et al. 2005; Guénette et al. 2006). These ecosystem models could form the basis for initial work to determine how robust current single-species management strategies are to trophic interactions and whether management strategies that include some ecosystem features are likely to outperform current approaches. Moreover, this exercise will provide an initial way to identify key sources of uncertainty and hence focus data collection strategies. In particular, if the performance of the management strategies differs markedly depending on which of several processes are actually present, experiments could be designed to attempt to distinguish among the alternative hypotheses. This approach has been used to identify causes for the marked (and undesirable) changes in the composition of the fish community on Australia's Northwest shelf and which strategy is best suited to reverse this (Sainsbury 1991; Sainsbury et al. 1997). Similarly, simulations were used to develop the current decision rule for Pacific sardine (*Sardinops sagax caerulea*) (Anonymous 1998*b*). This decision rule sets the target fishing mortality as a function of temperature because productivity of sardine has been shown to depend on temperature.

Evaluating current management strategies using existing ecosystem models as operating models may provide results of immediate use for EBFM. For example, Schweder et al. (1998) used a simple ecosystem model to assess the implications of achieving the management goals for baleen whales on likely sustainable yields for commercially important fish species. Also, Punt and Butterworth (1995) evaluated the impact of seal culls off South Africa on fish yields when the total allowable catches (TACs) for the fish species were based on the actual management strategies for these species. Similar analyses have yet to be conducted for the areas managed by the PFMC and NPFMC even though ecosystem models are available for these regions. Although the implications of simple management strategies (e.g., constant effort) have been examined using existing ecosystem models (Kitchell et al. 2002), such strategies do not adequately mimic how (single-species) management operates in reality. Only by evaluating the strategies as they are actually implemented by the FMCs will the necessary insights be achieved.

A necessary research activity to evaluate management strategies based on current ecosystem models is to expand these models so that they represent species at the same resolution as stock-assessment models (i.e., usually by age and sex). Age structure has already been added to some ecosystem models (Aydin 2004), but this is not the norm. Expanding beyond examining the implications of trophodynamics requires the construction of system models that are spatially explicit. Spatial models already exist that include trophodynamics and that could form the basis for MSE evaluations (Fulton et al. 2005). While these models are unlikely to be sufficient to evaluate all likely management strategies, the insights gained using such models at this early stage will provide decision makers with ideas regarding the way in which management strategies will have to be modified to better achieve management goals that include ecosystem considerations.

Goodman et al. (2002) suggested the need for metrics of ecosystem status in evaluating the success of EBFM. These metrics could be used as the basis for status thresholds to assess whether ecosystems are becoming unhealthy. An example of a set of ecosystem-based metrics from Murawski

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(2000) is as follows: (1) The biomass of one or more important species assemblages or components falls below minimum biologically acceptable limits, such that (*a*) recruitment prospects are substantially impaired, (*b*) rebuilding times to levels allowing catches near maximum sustainable yield are extended, (*c*) prospects for recovery are jeopardized because of species interactions, and (or) (*d*) any species is threatened with local or biological extinction. (2) Diversity of communities or populations declines substantially as a result of sequential "fishing-down" of stocks, selective harvesting of ecosystem components, or other factors associated with harvest rates or species selection. (3) The pattern of species selection and harvest rates leads to greater year-to-year variation in populations or catches than would result from lower cumulative harvest rates. (4) Changes in species composition or population demographics as a result of fishing greatly decrease the resilience or resistance of the ecosystem to perturbations arising from nonbiological factors. (5) The pattern of harvest rates among interacting species results in lower cumulative net economic or social benefits than would result from a less intense overall fishing pattern. (6) Harvests of prey species or direct mortalities resulting from fishing operations impair the long-term viability of ecologically important, nonresource species (e.g., marine mammals, turtles, and seabirds).

Adopting such metrics for ecosystem status would help management bodies manage fisheries sustainably and provide thresholds for measuring their success.

Discussion — the next steps

Many years will be required for implementation, testing, and adaptation of EBFM. However, there are ways of moving forward with most of the elements above. As a start, management bodies need to create and implement processes and institutional structures that will facilitate the identification of the full range of goals, especially those related to concerns beyond targeted species, and to make these operational.

There are also activities, such as using models to identify critical data gaps, and ecological processes that could be implemented immediately. Furthermore, ecosystem models should be developed to identify areas of high uncertainty and hence guide research and data collection. It is also important to encourage a modeling culture that rigorously quantifies the predictive power of all the models that are utilized, so that managers can make informed decisions when they consider using these models to guide actual management. It should be expected that the models on which scientific management advice is based would evolve over time from population models (single-species) to community models (taking into account food web considerations) and then to ecosystem models (taking into account environmental considerations such as habitat and climate).

Additionally, as research progresses, the fishery management approach will evolve from implicit and nonquantitative consideration of the ecosystem to a more specific and explicit quantification. It will also progress from treating ecosystem considerations outside fishery assessment and management to where these considerations are fully integrated into the process (Goodman et al. 2002).

Until the necessary research is done, it is not possible to know what the optimal management tools and their data requirements will be for EBFM. It could be that a set of single-species models combined with a collection of ecosystem indicators and prudent management strategies could suffice for many systems. For other systems, it may be necessary to develop complex ecosystem models with links among fish species, oceanography, climate, habitat, and human elements. It is also possible that the lofty goals of understanding the ecosystem and managing human uses sustainably are not fully achievable with finite resources and modeling capabilities. In that case, the goal may have to be limited to an achievable one, in which the risks of ecosystem harm are minimized through robust management strategies that set margins of safety for errors due to incomplete understanding.

Clearly the task of progressing towards EBFM will be difficult and will require substantial new investments. Management that takes ecological and ecosystem effects into account will require greatly expanded monitoring; improvement in the understanding of behavioral relationships among fishermen, the fish they catch, and the predators and prey of the harvested species; and social and economic relationships among various resource users. Additional funding and resources will be needed to get this work done. The benefits will be the explicit incorporation of societal goals in fishery management, more stable and predictable long-term yields, and the maintenance of ecosystem goods and services into the future.

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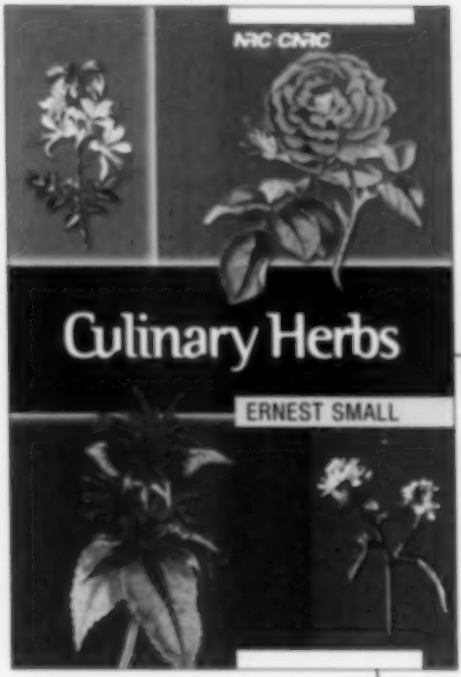

Culinary Herbs

2nd edition

By / Par
Ernest Small

1036 Pages 2006
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ISBN 0-660-19073-7; NRC 44467
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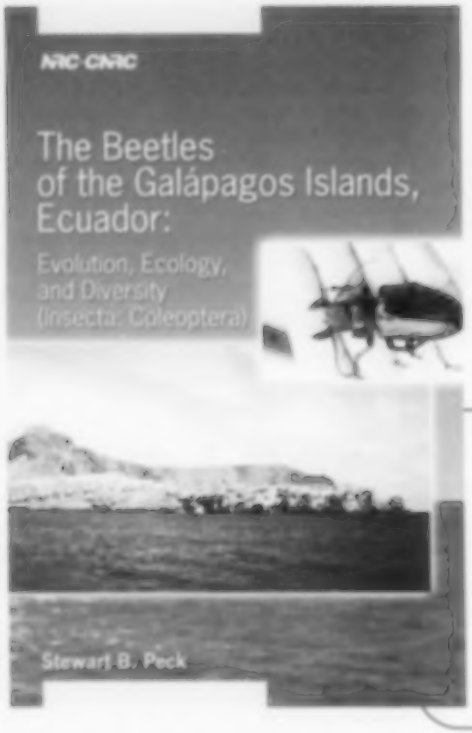
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Evolution, Ecology, and Diversity (Insecta: Coleoptera)
Stewart B. Peck

The Beetles of the Galápagos Islands, Ecuador:

Evolution, Ecology, and Diversity (Insecta: Coleoptera)

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Ludlow and Pridoli (Upper Silurian)

Graptolites from the Arctic Islands, Canada

By / Par
A. Lenz and A. Kozłowska-Dawidziuk

141 Pages 2004
Softcover / Édition brochée

ISBN 0-660-19326-4; NRC 46842
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Graptolites flourished from earliest Ordovician to Early Devonian, a time range of about 90 million years, and were widely distributed as marine benthic and planktonic colonial organisms around the world. They were diverse and rapidly evolving and, as such, make excellent "index fossils" for relative age-dating of their enclosing basinal rocks. Rarely, however, graptolites are beautifully preserved in their original three-dimensional form, and can be extracted from the enclosing rock for detailed study under scanning electron microscopy. Such a unique preservation is pervasive in the latest Ordovician to latest Silurian rocks of the central Arctic Islands of Canada, presenting an opportunity to study their complex morphology and evolution, making the Arctic graptolite sequence unique in the world. The present study examines the isolated, uncompressed as well as flattened forms from the Ludlow and Pridoli (Upper Silurian) graptolites of the Arctic, recognizing 46 species of monograptids and retiolitids of which seven are described as new species or subspecies.

Les graptolites abondaient entre le début de l'Ordovicien inférieur et le Dévonien inférieur, période d'environ 90 millions d'années, et étaient des organismes coloniaux marins benthiques et planctoniques largement répartis dans le monde. Leur diversité et leur rapide évolution en font des marqueurs stratigraphiques exceptionnels. Bien que ceci soit rare, on retrouve des graptolites superbement bien préservés, en trois dimensions, susceptibles d'être extraits de la roche et examinés par microscopie électronique à balayage. La période entre la fin de l'Ordovicien et la fin du Silurien dans l'archipel arctique canadien a été particulièrement favorable à cette extraordinaire préservation. La possibilité d'étudier leur morphologie complexe et leur évolution fait des Graptolites de l'Arctique des spécimens sans égal dans le monde. Dans cette étude, on examine les spécimens isolés et non comprimés de même que les empreintes fossiles de graptolites du Ludlow et du Pridoli (Silurien supérieur) de l'Arctique et on signale 46 espèces de monograptides et de rétiolitides, notamment sept constituant de nouvelles espèces ou sous-espèces.

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